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VEGETATIVE CHANGES AND GRAZING USE ON DOUGLAS FIR CUT-OVER LAND [1,2]

By DOUGLAS C. INGRAM

Late *Associate Range Examiner, Forest Service, United States Department of Agriculture*

INTRODUCTION

The protection from fire of Douglas fir cut-over areas in the region west of the Cascade Mountains in Oregon and Washington is an exceedingly difficult and expensive undertaking which is giving grave concern to landowners and foresters alike. In view of the large acreage in this region (more than 4,000,000 acres) in various stages of reforestation and of the fact that some 200,000 acres are added annually to this total, any method that will reduce the natural fire danger by the removal of the inflammable material is worthy of careful consideration.

Use by livestock of the natural forage produced on cut-over and burned-over areas during the early and critical stages of restocking is one important method of reducing fire hazard and at the same time of converting into valuable animal products a secondary forest resource which, if left, becomes a liability. This utilization of the land also gives promise of producing some revenue, which can be used to meet protection costs, interest charges, and taxes until such time as another crop of timber can be marketed. The development of correct grazing-management principles which will assist rather than interfere with reforestation on Douglas fir cut-over lands is, however, essential.

The Forest Service, in the course of studies of grazing management of Douglas fir cut-over areas in Washington and Oregon, devoted considerable attention to an analysis of the successional changes which occur in the vegetation, in an effort to determine the influence of varying degrees of grazing use on the density and composition of the vegetation. Study of the plants in the early stages of succession is important: (1) Because their presence in abundance creates an excessive fire hazard, rendering cut-over areas exceedingly susceptible to reburn; that is, to one or more burns other than the usual broadcast burn which is made soon after logging; and (2) such study is important because this vegetation has possibilities as feed for livestock, and its use and removal are means of reducing fire hazard.

The vegetation in its early successional stages is in reality a nurse crop for the climax type of vegetation. Owing to the density, uniformity, and composition of this early vegetation, grazing-manage-

[1] Received for publication Mar. 16, 1931; issued September, 1931.

[2] This report appears in a form only slightly modified from that in which it was prepared by the author a short time before his untimely death.

ment objectives on this type of range differ materially from those on strictly grazing areas where the central objective is the maintenance of a climax type of secondary vegetation permanently suited to grazing use.

In considering vegetational changes, therefore, and the influence of grazing on them, it is important to keep in mind the effect of grazing (1) in reducing the fire hazard, (2) in shortening or prolonging the grazing cycle, and (3) on reforestation.

In addition to the general study of vegetation made throughout the region since 1919, grazed transect plots on the Columbia National Forest in Washington have been examined periodically and checked with comparable ungrazed plots. On the area studied a transitory type of vegetation composed largely of fireweed (*Chamaenerion angustifolium*) and bracken (*Pteridium aquilinum pubescens*) came in rapidly after logging and burning, first by broadcast slash disposal and second by accidental burns. This early vegetation as well as that which follows is materially influenced by the intensity and season of the slash or other burn. In this study the effort has been made particularly to determine the influence of grazing on the successional trend of the vegetation and on the promotion of conditions favorable to the protection and development of forest tree seedlings. Variation in the understory is rather of proportional representation than of presence or absence of species.

THE UNDERSTORY OF VEGETATION BEFORE CUTTING

Because of the heavy shade which occurs in dense Douglas fir forests of the Pacific slope,[3] the understory of shrub and herbaceous species found surviving therein is inevitably limited to those species which are especially tolerant of shade and which likewise can be aided and protected by the modified temperature and moisture conditions common to dense forests. (Fig. 1.) The ability of these species to obtain nourishment from the soil under the intense root competition which prevails is also probably a factor of no mean importance.

Except where fire or other agencies have opened up the timber stand prior to cutting, the understory in aged timber stands is preponderantly of shrub species intermingled with conifer seedlings of various ages and species, mainly Douglas fir (*Pseudotsuga taxifolia*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), lowland white fir (*Abies grandis*), and Pacific yew (*Taxus brevifolia*). The most characteristic of these plants are the following, in the order of their usual abundance:

Shrubs: Salal (*Gaultheria shallon*), Oregon hollygrape (*Odostemon aquifolium*), hollygrapes, (*O. nervosus* and *O. repens*), locally called Oregon grape, vine maple (*Acer circinatum*), red, black, and blue huckleberry (*Vaccinium* spp.), pachistima, also called mountain lover (*Pachistima myrsinites*), and dogwoods (*Cornus nuttallii*, *C. occidentalis*, and *C. stolonifera*). Pacific dogwood (*C. nuttallii*) is properly a tree species but is usually suppressed under conifer stands.

[3] An excellent description of the Douglas fir type proper is given in the following publication: MUNGER, T. T. TIMBER GROWING AND LOGGING PRACTICE IN THE DOUGLAS FIR REGION. U. S. Dept. Agr. Bul. 1493, 42 p., illus. 1927.

Shrubs of lesser abundance, though still important in the type, are: Oceanspray (*Sericotheca discolor*), willows (*Salix* spp.), alder (*Alnus oregona*), hazel (*Corylus californica*), serviceberry (*Amelanchier florida*), spirea (*Spiraea menziesii*), snowbrush (*Ceanothus velutinus*), blackberry (*Rubus macropetalus*), whitebark raspberry (*Rubus leucodermis*), rose (*Rosa nutkana*), blueberry elder (*Sambucus caerulea*), bitter cherry (*Prunus emarginata*), rhododendron (*Rhododendron californicum*), tan oak [4] (*Lithocarpus densiflora*), golden chinquapin [4] (*Castanopsis chrysophylla*), and madrone [4] (*Arbutus menziesii*).

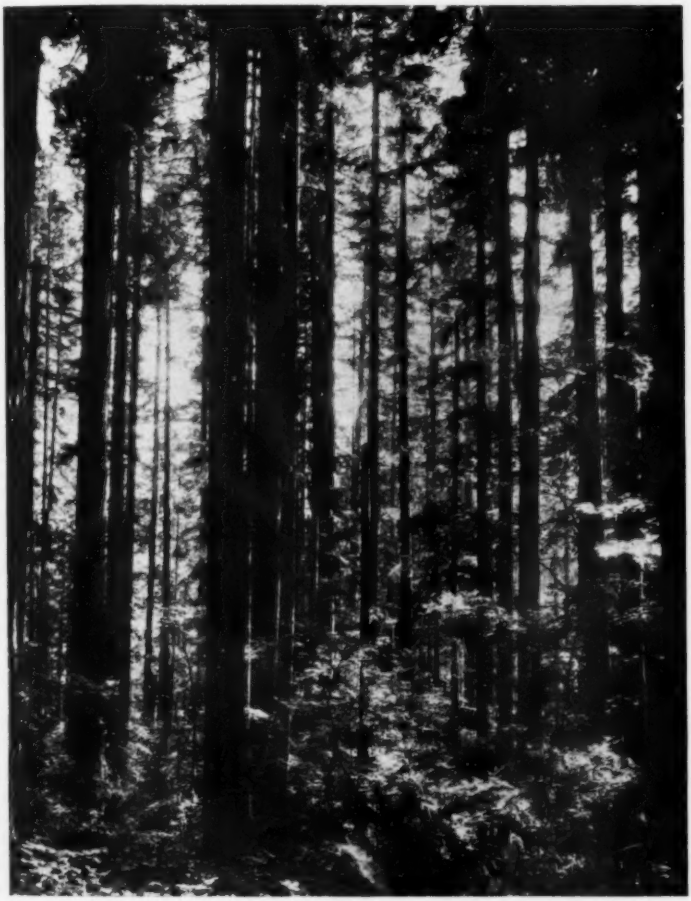

FIGURE 1.—Virgin stand of Douglas fir timber ready for the ax

[4] In the southern portion of the Douglas fir belt and along the coast, tan oak, golden chinquapin, and madrone are often important species in tree form.

Herbaceous species: Those found in the original type are: Vanilla leaf (*Achlys triphylla*), twinflower (*Linnaea borealis americana*), inside-out-flower (*Vancouveria hexandra*), beargrass (*Xerophyllum tenax*), anemone (*Anemone oregana*), pyrola (*Pyrola secunda, P. picta,* and *P. bracteata*), violet (*Viola* spp.), pipsissewa, often called princes' pine (*Chimaphila umbellata occidentalis*), Pacific trillium or wake-robin (*Trillium ovatum*), rattlesnake-plantain (*Peramium menziesii*), bracken, other true ferns (*Polypodium, Polystichum,* etc.), bunchberry or ground cornel (*Cornus canadensis*), fireweed, bishopscap (*Mitella* spp.), saxifrage (*Saxifraga* spp.), foamflower (*Tiarella* spp.), queencup (*Clintonia uniflora*), and starflower (*Trientalis latifolia*).

A number of other herbaceous species of minor importance also occur; it is the intent here merely to list those commonly found and generally recognized. Where the timber stand has been undisturbed, a number of the species named are found.

Shrub and herbaceous species which form the understory of vegetation in virgin timber on the Wind River section of the Columbia National Forest are fairly typical of the region as a whole. The principal species found on a belt transect, 2⅔ chains long and 6.6 feet wide, laid out and charted prior to logging in virgin timber on Falls Creek in this region in July, 1925, are given in Table 1.

TABLE 1.—*Record of principal shrubs and herbs composing understory on Falls Creek transect, 1925*

Species	Plants on transect		Acre equivalent	Species	Plants on transect		Acre equivalent
Shrubs:	*Number*	*Per cent*	*Number*	Herbs:	*Number*	*Per cent*	*Number*
Oregon hollygrape	716	49.90	26,850.0	Pipsissewa	162	61.3	6,075
Salal	468	32.61	17,550.0	Beargrass	32	12.1	1,200
Huckleberry	134	9.34	5,025.0	Pyrola	20	7.6	750
Pachistima	85	5.92	3,187.5	Violet	18	6.8	675
Serviceberry	14	.97	525.0	Anemone	12	4.6	450
Rose	7	.49	262.5	Vanilla leaf	8	3.0	300
Blackberry	5	.35	187.5	Trillium	6	2.3	225
Vine maple	3	.21	112.5	Others	6	2.3	225
Others	3	.21	112.5				
Total	1,435	100.00	53,812.5	Total	264	100.0	9,900

In view of the difference in size between species and individuals, numbers do not properly represent the ground cover each occupies. Tree trunks, fallen trees, and root and rock outcrops take up approximately 10 per cent of the soil surface. On the remaining 90 per cent there is a complete or 100 per cent density of shrubs and herbs. Because of the low forage value of most of the species the area is practically worthless for grazing. Not more than 3 per cent of the total growth of foliage and edible stems would normally be grazed under proper utilization of the more important species, and in a stand so dense it would be impossible to use even this amount.

The preponderance in virgin stands of shrubs of the type of salal and Oregon hollygrape is clearly shown in Figure 2.

The most striking points brought out by the examination and study of this transect are as follows: (1) The presence, in this climax type, of long-lived perennials only; (2) the preponderance of shrub, or at least woody plants, over herbaceous or succulent species; and (3)

the fact that this secondary vegetation in the uncut timber is largely unpalatable to livestock.

CHANGES ON FALLS CREEK TRANSECT AFTER BURNING AND LOGGING

The Falls Creek transect was burned over in an accidental fire in July, 1925, in which all the timber was killed. (Fig. 3, A and B.)

FIGURE 2.—The abundance of shade-tolerant species, such as salal and Oregon hollygrape, over herbaceous or succulent vegetation is indicated in this typical view of the original type taken on the Falls Creek transect, Wind River area, Columbia National Forest

The area was logged in 1926, the usual practice of logging followed by slash fire thus being reversed. The duff, moss, needles, and débris that originally covered the forest floor were completely burned away, exposing the roots of trees and shrubs, especially of the larger stumps. A number of the down trees originally charted and not consumed in the fire were removed in logging, together with small trees. All that remained of the original trees was the broken logs, limbs, and other

FIGURE 3.—A, Looking north on Falls Creek belt transect, Columbia National Forest, before the fire of July, 1925. This shows a virgin stand of timber and dense undergrowth and is typical of conditions in the Douglas fir forest before cutting. B, Same scene as Figure 3, A, after the fire of July, 1925, which killed the timber and eliminated the undergrowth. Note in foreground the stubs of shrubs killed by the fire

débris. In addition the ground was heavily scarred by log skidding. Figures 4 and 5, showing conditions on the first 30 feet of this transect before and after fire and logging, give some idea of the change which customarily takes place in the principal understory species when the conifer type is cut over and burned. Changes in the density and composition of the vegetation on this transect are given in Table 2, showing conditions on July 15, 1925, and September 26, 1928, respectively.

TABLE 2.—*Conditions on the Falls Creek transect in 1925 and 1928*

Surface conditions	1925	1928
	Per cent	*Per cent*
Surface available for plant growth	90	90
Density of all vegetation (other than tree growth on the surface available)	100	28
Density factor (density×surface)	90	25.2
Palatability of vegetation to livestock	3	25
Forage-acre factor (palatability×density factor)	.3	6.3

TABLE 3.—*Principal shrubs on Falls Creek transect in 1925 and 1928*

Shrub	1925	1928
	Number	*Number*
Oregon hollygrape	716	489
Salal	468	176
Pachistima	85	28
Huckleberry	134	18
Total	1,403	711

A comparison of Table 3 with Table 2 will show that while the total number of important shrub species was reduced one-half from 1925 to 1928 the actual density of the vegetation as a whole, other than the growth, was reduced from 90 to 25 per cent, or a density reduction of 65 per cent.

The increase in the palatability of the vegetation is explained in the appearance of fireweed, hawkweed (*Hieracium* sp.), and other palatable species, immigrants in the type. At the same time opening up the transect by fire and logging made the forage more accessible. Conifer seedlings of all ages and species found on this transect prior to burning and logging totaled 146 for the transect, or 5,475 per acre. Burning and logging eliminated these entirely. By September, 1928, only 18 (or 675 per acre) western white pine, Douglas fir, and hemlock seedlings one-half to 2½ years old were found on the transect.

ADVERSE EFFECT OF SITE CHANGE ON SURVIVORS

The adverse effect on vegetation of changes in light, heat, and moisture resulting directly from the removal of the protective timber cover is strikingly illustrated in the changes that take place in the survivors in their effort to adjust themselves to this sudden change in environment. Vine maple, huckleberry, and rose are conspicuously suppressed in size and growth habit, with smaller leaves and more compact form. Such low plants as trailing violet (*Viola sarmentosa*), greencup, and bunchberry, which reach their best development in the virgin timber type, occasionally occur on cut-over

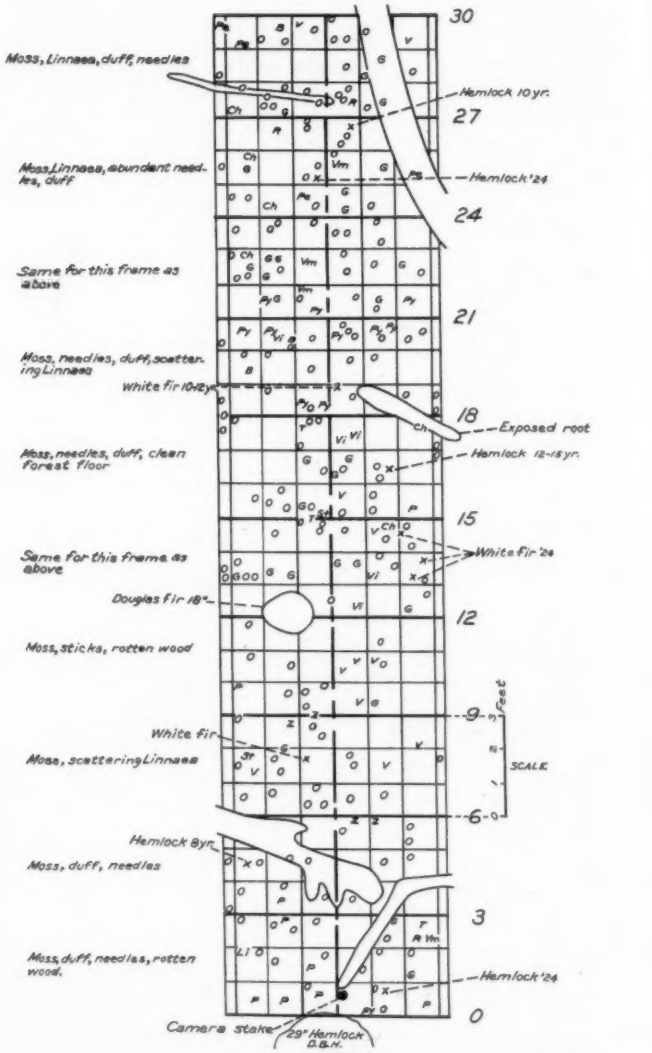

FIGURE 4.—First 30 feet of the Falls Creek transect before fire and logging

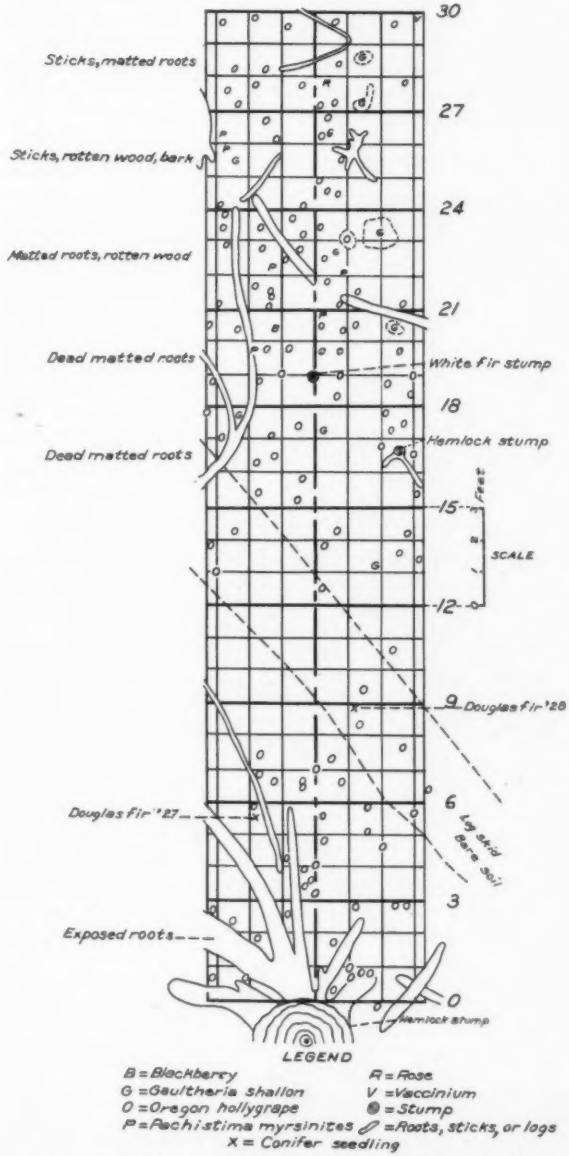

FIGURE 5.—First 30 feet of the Falls Creek transect after fire and logging

land but are greatly reduced in size, almost acaulescent, and with smaller, thicker, inrolled leaves. The recovery and response of these plants as shade increases and the succession advances is one of the most interesting features of cut-over land succession.

The factors which militate to prevent immediate reestablishment of the original vegetation have their effect also on reforestation, as is shown by heavy mortality of new conifer seedlings.

VEGETATIVE CHANGES ON CUT-OVER AREAS

The cutting and removal of timber on Douglas fir areas and the subsequent broadcast slash burn result in a profound ecological change. The mechanical disturbance of the soil by logging with powerful machinery and the destructive effect of intense heat engendered by the customary burn tend to eliminate much of the secondary vegetation found as an understory in the original forest. Only those individuals whose root crowns are in some manner protected survive. The degree of completeness with which the original type is eliminated and the composition of the subsequent vegetation are materially affected by the time, variation in the degree of heat, and completeness of the slash burn. After growth starts the hotter portions of the fire can be traced rather definitely by the presence of stubs and the absence of sprouting shrub species.

PRINCIPAL SPECIES IN EARLY SUCCESSION

In general, the vegetation immediately following the slash fire is in an elementary stage, certain mosses (*Polytrichum juniperinum*, *Ptilium crista-castrensis*, and *Funaria hygrometrica*), and liverwort (*Marchantia polymorpha*) appearing first. This stage is followed rapidly by the first weed stage, when the vegetation is composed of annuals and short-lived perennials; and this, in turn, is followed as rapidly by an association of shrub species and seedlings. The ashy and highly fertile seed bed left by the fire appears ideal for the reception and germination of wind-blown seed, and within one or two years the area is completely covered with a vigorous herbaceous vegetation composed principally of invading species interspersed scatteringly (sometimes frequently) with coppice from the shrubs which have survived the fire. The abundance, height growth, and density of this vegetation are among the most striking and interesting phenomena in the vegetative-replacement cycle. It is during this early stage, because of the accumulation of dense masses of dead vegetation, that cut-over Douglas fir areas are peculiarly susceptible to reburn.

In the reestablishment of the vegetative cover, certain herbaceous and shrub species, owing to their abundance, robust habit, vitality, and rapidity of growth, stand out conspicuously as major components in the first weed stage; however, as might be expected over so extensive a region as that covered by the Douglas fir type and its subtypes, no one species or group of species predominates throughout in this stage of succession. Fireweed, bracken (fig. 6), and trailing blackberry are without doubt by far the most frequent and abundant. These three species, which are frequently associated, occur in abundance on cut-over areas from northern Washington to southern Oregon and from sea level to the middle Cascades at 4,000-feet elevation.

Groundsel (fig. 7) may be the dominant invader over considerable areas in certain sections. In other sections lanceleaf thistle (*Cirsium lanceolatum*), pearl everlasting (*Anaphalis margaritacea*), or Scotch broom (*Cytisus scoparius*) may predominate; in many sections of the coast region in Oregon *Ceanothus thyrsiflorus* is one of the first and most persistent shrub species to occupy cut-over areas to the practical exclusion of other species. Snowbrush also occupies areas burned, though it usually comes into the cut-over stand in abundance later in the cycle. One significant feature common to all these encroaching

FIGURE 6.—Fireweed (*Chamaenerion angustifolium*) and bracken (*Pteridium aquilinum pubescens*), early invaders of Douglas fir cut-over land which have remained on this area even after a new stand of fir seedlings has become established

species is their apparent indifference to site limitation, such as difference in soil, slope, or aspect.

With the exception of bracken, which is propagated by spores, all the invaders are prolific seeders, and many of them are perennials. (Fig. 8.) The abundance of a single species or a combination of species appears to be accidental rather than a direct result of the ecological condition of the type itself. Careful study over a period of years has been given to the development of this transient vegetation and its effect on and relation to the future timber crop under grazed and ungrazed conditions.

On the transect established on cut-over land in the Wind River area on the Columbia National Forest the three species most common in the early vegetative stages were fireweed, comprising 40 per cent of the stand; bracken, 24 per cent; and blackberry, 7 per cent, a total of 71 per cent of all vegetation found. Because of the importance of such a primary species as fireweed, a rather careful study of its relationship to succession was made from 1925 to 1928 throughout the

FIGURE 7.—Groundsel (*Senecio vulgaris*), one of the common early invaders of Douglas fir cut-over areas

Douglas fir region. Most of the observations were on cut-over land at comparatively low elevations, from sea level up to 2,000 feet.

FIREWEED

Fireweed, well named from its association with burned-over areas, is a native short-lived perennial persisting in quantity for five to eight years on cut-over areas. (Fig. 9.) Typically a member of the Epilobium group of the Onagraceae (listed by some botanists as an Epilobium), the plant is characterized by its abundance, its robust

upright habit of growth (it becomes from 4 to 9 feet tall), its roughly symmetrical tapering spike crown bearing from 10 to 25 purple-pink blossoms, and its prolific propagation by rootstocks and seed. (Fig. 6.)

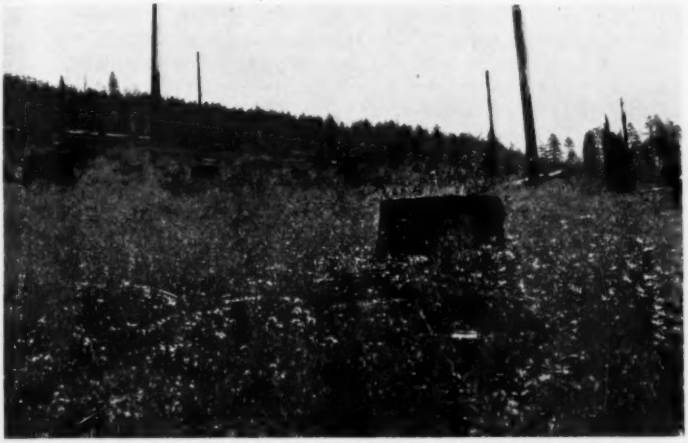

FIGURE 8.—A mixture of senecio, fireweed, thistle, bracken, and other species three years after logging

Though rarely found in the original forest, it is one of the first plants to appear in abundance on areas burned over. It flowers throughout July and August. On the Wind River area during 1925 and 1926, annual growth commenced and seed germinated about March 20 or

FIGURE 9.—Heavy stand of fireweed on cut-over area two years after logging and burning, Columbia National Forest

25. The flowering period was from July 10 to August 1, and seed dissemination began about July 25.

Fireweed is a prolific seeder, maturing seed from mid-July to September 10. The seed is scattered far and wide by the wind. During the period of greatest seed dissemination, usually the first

half of August, the air is filled with the light, cottony seeds, which in a light breeze are borne for miles. Few areas cut over and burned escape this invasion. The seeds find ideal lodgment in the ashes of a new burn, which apparently aid germination and stimulate the plant to its most robust growth. In two seasons a cover overtopping other plants and shrubs to the apparent exclusion of other forms of vegetation is formed. Under such conditions, if the soil is reasonably fertile, the plant grows from 7 to 9 feet tall.

Despite its great seeding capacity, fireweed after establishment appears to propagate principally from subterranean, progressive rootstocks which bud along their length and send up new stems. The season's growth above ground and the older portion of the rootstocks die annually. A definite rootstock is formed the first season of growth. During that season the plants usually attain, under favorable soil conditions, a height of 2 to 3 feet and a rootstock growth twice as great. A 4-year-old rootstock has been traced for a distance of 20 feet, and as many as 56 undeveloped buds have been found on it. The average is probably far less than this. The length depends on soil fertility and competition. Rootstock development apparently reaches its maximum about the second or third year and thereafter is believed to decline. The plant's ability to withstand competition is probably limited, for as other plants encroach it declines both in quantity and size and in 8 to 12 years is a minor constituent of the vegetation.

Bees and other insects are particularly attracted to the plant in bloom, and it is well known as a nectar producer. In the coast sections of Oregon and Washington apiarists follow the logging operations, moving every five to seven years to newer cut-over areas where this plant is more abundant. Although only moderately palatable to cattle, fireweed has high value as a forage plant for sheep, especially in association with other forage plants. When other feed is available fireweed is readily eaten at any stage of its growth, although four years' experience on the Columbia National Forest indicates that its most palatable stage is at full bloom. When it is the principal feed sheep become restless and unmanageable, craving a change in diet.

An interesting point in connection with the grazing of this plant is the effect of early grazing in apparently stimulating the plant to put forth growth of palatable sprouts which form a supply for fall use. Although there is no definite proof for the belief, it may be that the early grazing stimulates the development of the latent rootstock buds which under ordinary conditions might not develop until the following year. The ultimate effect is a lowering of vitality and hastening of the life processes, resulting in smaller stems and a lower height growth the ensuing year, and finally in a shorter life cycle.

Since this plant is one of those which materially increase the inflammability of cut-over lands, the effect of grazing in suppressing and eliminating it is of particular importance.

The Brambles

In addition to trailing blackberry, probably the commonest and most widely distributed species, several other species of the genus Rubus are found on cut-over Douglas fir areas and throughout the Douglas fir region. Cutleaf (evergreen) blackberry (*Rubus lacinia-*

tus) occurs abundantly along the coast and in southern Oregon and occasionally elsewhere in the region. This plant has escaped from cultivation. *R. hesperius*, whose range is usually limited to eastern Oregon and Washington, is found in abundance on the Columbia National Forest cut-over area. All these species are trailing in habit, root at the nodes, spread over logs and débris, and encroach rapidly. They are grazed moderately by sheep and less by cattle. Whitebark

FIGURE 10.—Secondary successional stage on cut-over Douglas fir land: A, Encroachment of shrub species; B, the proportion of shrub species rapidly increases and vegetation changes to a more permanent type in the secondary stage. The principal species here are vine maple, snowbrush, huckleberry, rose, Oregon hollygrape, salal, and elder

raspberry also is present in places, and salmonberry (*R. spectabilis*) and thimbleberry (*R. parviflorus*), occurring as remnants of the original type, are quite common.

SECONDARY SUCCESSION

As time goes on, if reburns do not occur, the proportion of shrub species increases rapidly, and vegetation changes to a more per-

manent type. (Fig. 10, A and B.) Such shrub or tree species as vine maple, bigleaf or Oregon maple (*Acer macrophyllum*), snowbrush, huckleberry, rose, longleaf or Oregon hollygrape, pachistima, blueberry elder, and oceanspray become the dominants until the faster-growing conifer seedlings overtop all other vegetation. As succession advances the changes in the plant cover are effected more slowly.

EFFECT OF REPEATED FIRE ON THE VEGETATION

That repeated burns result in soil impoverishment and in slowing up the successional process of the secondary vegetation and of forest regeneration is apparent even to a casual observer. Less obvious is the considerable extent to which the intensity of the fire in the original burn and in the reburn accounts for the many apparent contradictions in the natural succession. The importance of the intensity of the fires makes an accurate fire history of the individual area desirable.

Damage to timber reproduction and other vegetation on cut-over areas by any form of grazing use fades into insignificance when compared with the loss of seed trees, seedlings, and other plants caused by recurring fires such as have occurred on parts of the area under study. The more study given to this problem, the more apparent it becomes that prevention of the reburn is the major solution to reforestation on cut-over Douglas fir areas.

Table 4 gives the logging and fire record for a number of 0.01-acre plots 1 chain long and 6.6 feet wide included in each of the various areas, designated A to G, along the Wind River transect. Logging and burn conditions on these areas are representative of the area as a whole.

TABLE 4.—*Number of plots and logging and fire history of areas A to G*

Area	Plots in each area		Year logged	Fire history
	Grazed	Ungrazed		
	Number	*Number*		
A	4	2	1919	Single fall slash burn Oct. 18, 1919.
B	8	2	1919	Single summer burn (accidental) July 8, 1919.
C	19	4	1919	Double burn (accidental) July 8, 1919, and May 15, 1924.
D	7	2	1919	Spring slash burn, May 4, 1920; accidental reburn, May 15, 1924.
E	21	4	1919	Single fall slash burn, Sept. 17, 1921.
F	20	2	1920	Fall slash burn, Sept. 17, 1921; accidental reburn (spotty) June 4, 1924.
G	10	4	1920	Single fall burn, Sept. 17, 1921.
Total	89	20		

Table 5 shows the density, or percentage of the ground covered by vegetation within reach of livestock, and the percentage of composition of each of the important species or groups in 1925 on areas cut over in 1919 and 1920 and burned once or twice.

The harmful effect of repeated burns on forage production is clearly shown by the lower density of vegetation and the higher percentage of bracken on areas C, D, and F where double burns occurred, as compared to areas A, B, and G where there were only single burns. Area E had but one known burn, but coming two years after logging, it had much the same effect as a reburn. It is also interesting to note the higher percentage of composition and density of such palatable plants as grasses, sedges, blackberry, maple, pea vine (*Lathyrus* spp.), rose, dogwood, lotus (*Lotus* spp.), hawkweed, willow, and elder on

areas where a single burn had occurred soon after logging than on those where a later single burn or reburn had occurred. Another illustration of the harmful effect of a reburn is afforded by a small burn in April, 1926. On the parts covered, all vegetation above ground was completely consumed, even to the few conifer seedlings present.

TABLE 5.—*Density and composition, in percentage, by important species and groups in relation to burns on areas A to G, 1925*

Density and species [a]	Density and percentage composition after—						
	One burn soon after logging						
	Area A		Area B		Area G		Average
	Grazed	Ungrazed	Grazed	Protected	Grazed	Protected	
Density	56.6	57.2	72.3	73.5	34.3	37.8	50.4
Species:							
Fireweed	48.8	42.5	17.0	17.0	31.0	53.7	32.6
Bracken			.1		22.0		7.4
Grass-sedge	7.8	8.0	21.4	25.0	1.2		9.3
Blackberry	31.2	35.0	6.3	5.0	9.8	3.8	12.3
Maple	2.8	.5	8.8	10.0	8.0	8.8	7.2
Pea vine			27.5	32.5			9.5
Oregon hollygrape					7.0	7.5	3.3
Rose	.8	.5	.6		10.3	1.2	3.9
Salal					1.7	7.8	1.6
Dogwood					4.1	5.0	2.0
Lotus			10.6	2.5			3.0
Huckleberry	.2	.5			.1	3.5	.6
Hawkweed	.5	.5	.8	2.5	.1	.5	.6
Willow	3.5	5.0	.8				1.0
Epilobium					.1		
Hazel	.2	.5	.1		2.0		.8
Elder			1.6				.4
Pearl everlasting	.2				.1		.1
Others	4.0	7.0	4.4	5.5	2.5	8.2	4.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Density and species [a]	Density and percentage composition after—									
	One burn two years after logging			Two burns						
	Area E			Area C		Area D		Area F		
	Grazed	Protected	Average	Grazed	Protected	Grazed	Protected	Grazed	Protected	Average
Density	23.8	19.4	23.1	34.8	32.7	17.4	19.6	28.0	23.4	28.9
Species:										
Fireweed	31.4	27.5	30.8	51.0	58.8	37.4	47.5	50.0	17.5	48.2
Bracken	39.0	36.2	38.6	25.1	25.0	30.0	32.5	28.3	47.5	28.1
Grass-sedge	1.9	.8	1.7	9.0	3.2	.3		.7	2.5	3.8
Blackberry	6.8	1.8	6.0	5.4	5.5	3.0	4.0	7.0	5.0	5.7
Maple	2.3	7.5	3.2	.3	1.2	10.0	5.0	2.8	7.5	3.0
Oregon hollygrape	3.7	5.5	4.0	.1		2.3	3.0	3.2		1.6
Rose	1.5		1.3	.8		3.3	4.0	.9		1.2
Salal	1.8	1.8	1.8	.3		1.6	.5	.9	(b)	.6
Dogbane	6.3	13.8	7.5	1.0		8.0	.5	.1		1.5
Dogwood	1.2		1.0	.1	(b)			1.6	5.0	.8
Lotus				.1						
Groundsel	.1	.2	.1	.3	.5	.9		.6	5.0	.6
Huckleberry	1.0	3.7	1.5	.7		.6	.5	.2	(b)	.4
Hawkweed	.2		.1	.5	.5	.1		.2		.2
Willow				.6	2.5					.4
Epilobium	.1					.9		1.2	10.0	.9
Hazel	.2		.2							
Elder				.1				.2	(b)	.1
Pearl everlasting	.1	.2	.1	.1		(b)			(b)	
Others	2.4	1.0	2.1	4.5	2.8	1.6	2.5	2.1		2.9
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

[a] Density is given in percentage of ground covered. Figures for species represent percentage of composition.

[b] Less than one-half per cent.

The prevalence of nonpalatable but under certain conditions highly inflammable bracken on reburns has been repeatedly noted and is probably the best indicator of reburn conditions. (Fig. 11.) The abundance of bracken is probably evidence rather of the superior ability of this species to survive than of any direct stimulus from the burn. Reburns are highly injurious to other species and gradually eliminate the less resistant. The deep-rooted and persistent rootstocks of bracken are protected from the fire, and following the removal of competing species find ideal conditions (in which to send forth new shoots to thrive, produce, and germinate spores) such as those that were so attractive to other invading species in the first successional stages. On the areas studied in 1925 bracken formed on 0.01 acre (chain) plot 90 per cent of the total vegetation actually produced, and on 21 other plots along the transect (mainly on areas D and E) it amounted to 50 per cent or more of the total vegetation.

Broadly it may be said that the areas of single burns, A, B, and G, have produced in the last four years a greater quantity of palatable

FIGURE 11.—Near the edge of an area repeatedly burned. Note the abundance of bracken

vegetation to the acre than the areas where reburns occurred and so have received greater grazing use.

CHANGES UNDER PROTECTION FROM GRAZING 1925 TO 1927

Table 6 shows in summary form for each of the seven type areas of the Wind River transect the changes in actual density of species occurring from 1925 to 1927 under protection from grazing.

On the average the total density of the vegetation on the ungrazed plots declined 13.3 per cent from 1925 to 1926, and 21.4 per cent from 1925 to 1927. Area A, with a relatively high density in 1925, showed the greatest reduction to 1927. This was accounted for largely by the reduction (over 80 per cent) in density of fireweed. All the other areas, with the exception of area F which had a small increase, showed a reduction in the proportion of fireweed sufficient in most cases to account for most of the reduction in density of all the vegetation on each area as a whole. On areas D and F increases in density occurred; on D large increases in blackberry and maple more than offset large decreases in fireweed and bracken.

TABLE 6.—*Actual densities, in percentage of ground covered, by species or groups and type areas, 1925 to 1927, ungrazed plots*

Species	Actual density on area A				Actual density on area B			
	1925	1926	1927	Percentage change 1925 to 1927	1925	1926	1927	Percentage change 1925 to 1927
Fireweed	24.42	7.10	4.35	−82.2	12.38	3.15	1.77	−85.7
Bracken		.40	.36					
Grass-sedge	4.49	3.87	4.10	−8.7	18.00	11.33	9.67	−46.3
Blackberry	19.98	17.06	14.89	−25.5	3.60	7.28	4.66	+29.4
Maple	.28				7.50	11.47	12.11	+61.5
Pea vine					24.37	21.04	15.34	−37.1
Rose	.28					.38	.40	
Lotus					1.80	1.38	1.19	−33.9
Groundsel						.77	.81	
Huckleberry	.28	1.36	1.02	+264.3				
Hawkweed	.29	2.10	2.28	+686.2	1.80	2.21	1.70	−5.6
Willow	2.92	1.70	1.53	−47.6				
Epilobium						.38	.40	
Hazel	.28							
Elder						.38	.40	
Thistle		.17	.63			1.92	4.04	
Others	[a]4.03	3.24	1.59	[b]44.9	[a]4.05	4.19	4.89	[b]+120.5
Total density	57.25	37.00	30.75	−46.3	73.50	65.88	57.38	−21.9

Species	Actual density on area C				Actual density on area D			
	1925	1926	1927	Percentage change 1925 to 1927	1925	1926	1927	Percentage change 1925 to 1927
Fireweed	21.40	8.52	5.87	−72.6	9.69	3.40	1.27	−86.9
Bracken	4.38	1.23	1.33	−69.6	5.85	1.70	1.27	−78.3
Grass-sedge	1.66	3.12	3.94	+137.3				
Blackberry	2.17	3.15	4.07	+87.6	.80	9.52	8.42	+952.5
Maple	.64				1.07	11.90	8.93	+734.6
Oregon hollygrape					.62	1.70	1.27	+104.8
Rose		.07	.07		.80	5.10	3.82	+377.5
Salal		.02	.02		.10			
Dogbane					.10			
Dogwood		.11	.10					
Lotus		.09	.08					
Groundsel	.25	.47	.61	+144.0		.34	.26	
Huckleberry		.11	.10		.11			
Hawkweed	.25	.27	.44	+76.0				
Willow	1.28	1.35	1.60	+25.0				
Epilobium		.03	.04					
Pearl everlasting		.09	.08					
Others	.67	.87	2.15	+220.9	.48	.34	.26	−45.8
Total density	32.70	19.50	20.50	−37.3	19.62	34.00	25.50	+30.0

[a] Includes density of thistle.
[b] Percentage of change includes total of "others" plus thistle in 1927.

TABLE 6.—*Actual densities, in percentage of ground covered, by species or groups and type areas, 1925 to 1927, ungrazed plots*—Continued

Species	Actual density on area E				Actual density on area F			
	1925	1926	1927	Percentage change 1925 to 1927	1925	1926	1927	Percentage change 1925 to 1927
Fireweed	3.46	1.45	1.23	−64.5	5.42	3.44	6.42	+18.5
Bracken	8.14	8.72	6.75	−17.1	9.24	9.58	11.95	+29.3
Grass-sedge	.07	.69	.74	+957.1	.32	.14	.20	−37.5
Blackberry	.32	1.99	1.64	+412.5	1.70	2.16	2.57	+51.2
Maple	1.91	3.04	3.86	+102.1	2.02	.47	.54	−73.3
Oregon hollygrape	.61	.40	.63	+3.3	.....	.14	.20	.....
Rose	.....	.19	.18	.....	.....	.....	.....	.....
Salal	.31	.20	.19	−38.7	.....	.14	.20	.....
Dogbane	3.77	1.01	.90	−76.1	.....	.....	.....	.....
Dogwood	.....	.....	.....	.....	1.70	1.35	2.02	+18.8
Groundsel	.07	.37	.36	+414.3	1.17	.81	.20	−82.9
Huckleberry	.47	.15	.23	−51.1	.....	.....	.....	.....
Hawkweed	.....	.14	.14	.....	.....	.....	.....	.....
Epilobium	.....	.03	.03	.....	1.81	.67	.68	−62.4
Elder	.....	.....	.....	.....	.....	.67	1.01	.....
Pearl everlasting	.06	.30	.30	+400.0	.....	.14	.20	.....
Thistle	.....	.12	.24	.....	.....	.....	.....	.....
Others	[a].18	.08	.33	[b]+216.6	.....	.54	.81	.....
Total	19.37	18.88	17.75	−8.4	23.38	20.25	27.00	+15.5

Species	Actual density on area G				Average density				
	1925	1926	1927	Percentage change 1925 to 1927	1925	1926	1927	Percentage change 1925 to 1926	Percentage change 1925 to 1927
Fireweed	21.97	19.40	11.36	−48.3	14.56	7.58	5.07	−47.9	−65.2
Bracken	.....	.....	.....	.....	4.01	3.16	2.97	−21.2	−25.9
Grass-sedge	.....	.....	.....	.....	2.62	2.30	2.33	−12.2	−11.1
Blackberry	.56	1.05	1.16	+107.1	3.22	4.84	4.43	+50.3	+37.6
Maple	2.60	2.65	2.75	+5.8	2.12	3.52	3.48	+66.0	+64.2
Pea vine	.....	.....	.....	.....	2.44	2.10	1.53	−13.9	−37.3
Oregon hollygrape	2.36	1.17	1.18	−50.0	.66	.50	.51	24.2	−22.7
Rose	.71	.37	.99	+39.4	.25	.67	.67	+168.0	+168.0
Salal	2.33	2.35	2.56	+9.9	.54	.53	.57	−1.9	+5.6
Dogbane	.....	.....	.....	.....	.76	.20	.18	−73.7	−76.3
Dogwood	1.80	2.83	3.08	+71.1	.53	.72	.84	+35.8	+58.5
Lotus	.....	.....	.....	.....	.18	.16	.14	−11.1	−22.2
Groundsel	.....	.06	.05	.....	.18	.37	.33	+105.6	+83.3
Huckleberry	1.34	1.25	1.83	+36.6	.40	.44	.54	+10.0	+35.0
Hawkweed	.20	.83	.90	+350.0	.30	.68	.70	+126.7	+133.3
Willow	.....	.....	.....	.....	.55	.44	.47	−20.0	−14.5
Epilobium	.....	.....	.....	.....	.18	.12	.12	−33.3	−33.3
Hazel	.....	.....	.....	.....	.03	.....	.....	.....	.....
Elder	.....	.....	.....	.....	.....	.10	.14	.....	.....
Pearl everlasting	.....	.....	.....	.....	.01	.09	.10	+800.0	+900.0
Thistle	.....	.....	.....	.....	.....	.23	.52	.....	.....
Ceanothus	.....	.14	.21	.....	.....	.03	.04	.....	.....
Others	3.94	4.28	4.24	+7.6	[a]1.81	1.88	2.10	[c]+16.6	[b]+44.8
Total	37.81	36.38	30.31	−19.8	35.35	30.66	27.78	−13.3	−21.4

[a] Includes density of thistle.
[b] Percentage of change includes total of "others" plus thistle in 1927.
[c] Percentage of change includes total of "others" plus thistle in 1926.

INFLUENCE OF GRAZING ON PLANT COVER

GRAZING UTILIZATION

The degree of use of the range by sheep on the Columbia National Forest cut-over area was recorded on each of the eighty-nine 0.01-acre (chain) grazed plots along the Wind River transect. (Fig. 12.) Table 7 shows in summary form for each of the seven type areas the changes in actual density resulting on each area and for each species from 1925 to 1927, inclusive. The utilization records by species in percentage of foliage produced for 1925 and 1926 are also included. In determining the grazing value of individual species these utilization records were substantiated by more general observations and records taken on the whole area grazed on the Columbia National Forest and were also checked against observational notes for the region as a whole.

In addition to its value in gaging the palatability or proper degree of utilization of the individual plant species and of these species in

FIGURE 12.—Sheep grazing on the Wind River cut-over area, Columbia National Forest. Though at the time this picture was taken there were some 1,100 ewes with their lambs scattered over the area within the scope of the lens, the tall vegetation, principally fireweed, hid most of them. The logs aid in use of this rank vegetation

association with other plants, as a basis for determining carrying capacity, this record of utilization was found useful in checking adaptability of the range to the class of livestock grazed. Heavier utilization was found on the earlier cuttings, largely because of the general increase in plants of higher palatability as succession advanced and because the shrubs afforded shade for livestock. On such areas the palatable plants as a rule were more closely utilized, and more even utilization of all parts of the areas resulted. (Fig. 13.)

Fireweed, the most important species on the area, was grazed more closely on the older cuttings where it was less prominent and where other forage permitted variety in the diet. On newer cut-over areas where fireweed predominated, the sheep became restless, trailed a good deal, and were evidently looking for change of feed. Here shrub species were very closely utilized in an evident effort to break the monotony of the diet. Even some unpalatable shrubs such as snowbrush were grazed. On older cuttings, although shrubs

were present in greater proportions, their use was evidently lighter. In September after the lambs were weaned, more normal and even use of shrub species was made than during the summer, doubtless

FIGURE 13.—Sheep grazing on an older cut-over area; showing brush species and young conifers

owing to the more quiet grazing of the ewes following removal of the lambs, and the lack of more succulent feed at this time.

Grazing of palatable shrub and tree species, such as willow, black cottonwood (*Populus trichocarpa*), and blueberry elder, on the

FIGURE 14.—Shrubs trimmed by heavy grazing with sheep. The principal species is vine maple

Columbia area was largely limited to the part of the plant that could be reached by the sheep. (Fig. 14.) Logs were of importance and advantage in securing fuller utilization, as these enabled the sheep to reach the higher branches which normally would be unutilized. It was common to see from 3 to 10 lambs on one log, all

reaching for and feeding upon the higher and more succulent branches of some especially palatable shrub. Likewise tall fireweed was similarly grazed, some specimens to a height of more than 6 feet. On the Columbia study area, shrub species were utilized in 1925 to an average height of 4½ feet, and in many instances to 7 or 8 feet, resulting in a trimming-up process which in the case of 8 to 10 year old poplar and willow made for total elimination of the lower limbs.

TABLE 7.—*Actual densities, in percentage of ground covered, by species or groups and type areas, 1925 to 1927, and percentage of utilization of forage produced by species, 1925 and 1926, grazed plots*

Species	Actual density and utilization on area A						Actual density and utilization on area B					
	1925		1926		1927	Percentage change in density, 1925 to 1927	1925		1926		1927	Percentage change in density, 1925 to 1927
	Actual density	Utilization	Actual density	Utilization	Actual density		Actual density	Utilization	Actual density	Utilization	Actual density	
Fireweed	26.74	70.1	13.25	98.2	3.38	−87.4	11.24	90.8	3.38	99.7	0.92	−91.8
Bracken			.35	50.0	.90		.11					
Grass-sedge	4.61	71.0	3.91	97.7	4.48	−2.8	14.60	79.4	15.16	99.8	14.73	+.9
Blackberry	18.12	49.0	12.00	89.7	10.55	−41.8	3.70	61.4	3.12	91.5	2.40	−35.1
Maple	1.71	90.0	1.39	94.4	1.30	−24.0	6.90	95.0	7.46	96.0	7.04	+2.0
Pea vine							22.46	100.0	14.18	100.0	14.07	−37.4
Oregon hollygrape			.09	100.0	.07				.12	10.0	.10	
Rose	.45	85.4	.48	96.3	.54	+20.0	.41	76.4	.35	100.0	.35	−14.6
Dogbane			.04	75.0	.04							
Lotus			.17	100.0	.10		7.26	100.0	2.20	100.0	1.94	−73.3
Huckleberry	.14	65.0	.66	92.3	.57	+307.1						
Hawkweed	.27	86.3	.07	100.0	.04	−85.2	.53	100.0	.42	100.0	.86	+62.3
Willow	2.06	71.2	.77	96.8	.74	−64.1	.59	95.4	.41	92.8	.37	−37.3
Hazel	.14	50.0	.45	75.0	.70	+400.0	.09	10.0	.15	90.0	.14	+55.6
Elder							1.22	91.7	.47	100.0	.93	−23.8
Pearl everlasting	.12		.04	75.0	.04	−66.7						
Thistle			.24	100.0	.28				.56	100.0	.85	
Serviceberry			.09	95.0	.07				.15	95.0	.10	
Ceanothus									.17	28.8	.16	
Others	2.26	59.3	.62	95.0	.88	*−45.6	3.20	74.4	1.32	95.7	2.88	*+19.7
Total	56.62		34.62		24.68	−56.4	72.31		49.62		47.84	−33.8

Species	Actual density and utilization on area C						Actual density and utilization on area D					
	1925		1926		1927	Percentage change in density, 1925 to 1927	1925		1926		1927	Percentage change in density, 1925 to 1927
	Actual density	Utilization	Actual density	Utilization	Actual density		Actual density	Utilization	Actual density	Utilization	Actual density	
Fireweed	17.44	85.7	5.74	93.0	1.90	−89.1	5.74	78.1	2.11	96.7	0.25	−95.6
Bracken	7.60	1.0	9.56	23.4	9.65	+27.0	4.60		8.07	15.6	8.07	+75.4
Grass-sedge	4.15	94.7	4.78	99.0	5.60	+34.9	.05	50.0	.03	100.0	.21	+320.0
Blackberry	2.15	63.4	4.14	82.0	4.96	+130.7	.46	54.5	2.25	83.6	2.14	+365.2
Maple	.13	99.0	.34	96.1	.31	+138.5	2.58	68.8	2.19	90.6	2.10	−18.6
Oregon hollygrape	.02		.23	38.4	.24	+1,100.0	.42	10.1	.63	10.0	.66	+57.1
Rose	.32	90.0	.24	67.1	.24	−25.0	.72	83.7	.44	89.2	.46	−36.1
Salal	.08		.26	23.7	.22	+175.0	.39	54.9	.68	5.0	.80	+105.1
Dogbane	.32	7.5	.30	67.1	.30	−6.2	1.82	15.9	.79	95.4	.67	−63.2
Dogwood	.03	50.0	.26	68.8	.07	+133.3					.02	
Lotus	.06	90.0	.28	100.0	.18	+200.0						
Groundsel	.13	52.6	.29	100.0	.43	+230.8	.11	53.7	.09	100.0	.07	−36.4
Huckleberry	.23	50.0	.09	71.4	.12	−47.8	.07	60.0	.14	76.7	.19	+171.4
Hawkweed	.21	82.3	.06	100.0	.44	+109.5	.02	50.0			.08	+300.0
Willow	.28	95.3	.20	95.5	.16	−42.9						
Epilobium							.09	50.0	.04	100.0	.03	−66.7
Hazel					.04							
Elder	.06	90.0	.02	100.0	.06							
Pearl everlasting	.06				.02	−66.7						
Serviceberry			.15	75.0	.12							
Others	1.53	61.9	.46	95.6	.92	*−32.0	.28	44.6	.18	96.4	.21	−25.0
Total	34.80		27.40		25.98	−25.3	17.35		17.64		15.96	−8.0

* On basis of 1927 amounts for others plus thistle and serviceberry since these two species were included in others in 1925; likewise for total average 1926.

TABLE 7.—*Actual densities, in percentage of ground covered, by species or groups and type areas, 1925 to 1927, and percentage of utilization of forage produced by species, 1925 and 1926, grazed plots*—Continued

Species	Actual density and utilization on area E						Actual density and utilization on area F					
	1925		1926		1927	Percentage change in density, 1925 to 1927	1925		1926		1927	Percentage change in density, 1925 to 1927
	Actual density	Utilization	Actual density	Utilization	Actual density		Actual density	Utilization	Actual density	Utilization	Actual density	
Fireweed	7.39	75.8	4.54	32.2	2.72	−63.2	15.54	47.3	9.91	42.4	6.92	−55.5
Bracken	8.75	1.4	11.61	13.4	11.26	+28.7	6.54	.5	6.84	18.1	6.57	+.5
Grass-sedge	.34	88.4	.27	97.7	.76	+123.5	.15	61.0	.20	85.0	.23	+53.3
Blackberry	1.57	68.2	2.52	26.9	2.50	+59.2	1.89	41.8	2.52	36.1	2.24	+18.5
Maple	.72	62.9	.81	72.5	.87	+20.8	.79	58.2	.62	49.0	.67	−15.2
Oregon hollygrape	.83	85.7	.82	5.0	.90	+8.4	.95	5.0	1.04	.....	.96	+1.1
Rose	.31	3.9	.41	67.1	.44	+41.9	.38	79.0	.28	59.3	.34	−10.5
Salal	.41	50.0	.66	5.0	.81	+97.6	.20	20.1	.40	.....	.41	+105.0
Dogbane	2.44	14.8	1.25	80.3	.81	−66.8	.03	.....	.18	56.2	.25	+733.3
Dogwood	.28	80.5	.24	25.0	.29	+3.6	.37	61.2	.59	37.9	.59	+59.5
Groundsel	.01	90.0	.61	84.6	.14	+1,300.0	.12	81.0	.22	80.0	.14	+16.7
Huckleberry	.17	87.3	.15	27.6	.02	−88.2	.05	50.0	.12	23.2	.11	+120.0
Hawkweed	.03	81.8	.06	100.0	.29	+866.7	.05	50.0	.16	98.3	.30	+500.0
Willow	.....	.....	.....	.....	.....	.....	.01	.....	.08	87.0	.05	+400.0
Epilobium	.01	80.0	.....	.....	.....	.....	.23	76.3	.26	84.5	.25	+8.7
Hazel	.06	80.0	.05	46.3	.09	+50.0	.....	.....	.....	.....	.....	.....
Elder	.....	.....	.....	.....	.....	.....	.11	90.0	.04	95.0	.04	−63.6
Pearl everlasting	.01	70.0	.03	42.5	.06	+500.0	.02	.....	.02	.....	.04	+100.0
Ceanothus	.....	.....	.....	.....	.....	.....	.01	50.0	.05	.....	.05	+400.0
Others	.51	62.0	.55	79.6	.56	+9.8	.56	35.9	.55	53.8	.63	+12.5
Total	23.84	.....	24.58	.....	22.52	−5.5	28.00	.....	24.08	.....	20.79	−25.8

Species	Actual density and utilization on area G						Average						
	1925		1926		1927	Percentage change in density, 1925 to 1927	1925		1926		1927	Percentage change in density, 1925 to 1926	Percentage change in density, 1925 to 1927
	Actual density	Utilization	Actual density	Utilization	Actual density		Density	Utilization	Density	Utilization	Density		
Fireweed	12.22	75.2	7.14	41.8	5.25	−57.0	13.00	71.6	6.40	56.1	3.45	−50.8	−73.5
Bracken	4.98	.....	4.14	19.0	4.06	−18.5	6.09	1.0	7.43	18.0	7.29	+22.0	+19.7
Grass-sedge	.31	85.4	.25	88.4	.80	+158.1	2.56	84.3	2.70	98.9	3.06	+5.5	+19.5
Blackberry	4.30	73.7	5.75	50.4	4.14	−3.7	2.91	58.2	3.69	62.4	3.47	+26.8	+19.2
Maple	2.96	71.5	3.43	75.3	3.00	+1.4	1.61	79.1	1.69	84.1	1.62	+5.0	+00.6
Pea vine	.....	.....	.....	.....	.....	.....	2.02	100.0	1.27	100.0	1.26	−37.1	−37.6
Oregon hollygrape	2.25	9.1	1.18	.....	1.24	−44.9	.71	6.8	.67	23.7	.68	−5.6	−4.2
Rose	3.88	83.0	3.97	75.0	4.24	+9.3	.77	83.1	.75	74.4	.80	−2.6	+3.9
Salal	.42	20.0	.62	.....	.74	+76.2	.24	25.3	.43	13.3	.47	+79.2	+95.8
Dogbane	.....	.....	.....	.....	.....	.....	.79	14.4	.46	78.4	.37	−41.8	−53.2
Dogwood	1.14	79.7	1.04	31.4	1.17	+2.6	.28	74.1	.32	35.1	.35	+14.3	+25.0
Lotus	.....	.....	.....	.....	.....	.....	.66	99.8	.23	100.0	.22	−65.2	−66.7
Groundsel	.....	.....	.07	100.0	.06	.....	.06	67.7	.27	88.2	.17	+350.0	+183.3
Huckleberry	.03	50.0	.46	38.3	.46	+1,433.3	.11	63.1	.17	49.1	.19	+54.5	+72.7
Hawkweed	.03	95.0	.19	90.4	.64	+2,033.3	.12	88.5	.18	98.5	.38	+50.0	+216.7
Willow	.....	.....	.03	.....	.03	.....	.21	84.5	.14	94.0	.12	−33.3	−42.9
Epilobium	.03	90.0	.09	100.0	.08	+166.7	.06	73.8	.07	87.3	.07	+16.7	+16.7
Hazel	.95	60.3	.35	35.0	.50	−47.4	.13	59.1	.09	56.2	.13	−30.8	0
Elder	.....	.....	.....	.....	.01	.....	.15	91.2	.05	99.1	.10	−66.7	−33.3
Pearl everlasting	.03	50.0	.22	.....	.20	+566.7	.02	59.6	.04	48.8	.05	+100.0	+150.0
Thistle	.....	.....	.....	.....	.....	.....	.....	.....	.06	100.0	.09	.....	.....
Serviceberry	.....	.....	.....	.....	.....	.....	.....	.....	.05	82.2	.04	.....	.....
Ceanothus	.03	.....	.16	10.0	.17	+466.7	.04	50.0	.05	18.4	.04	+25.0	0
Others	.74	69.2	.35	74.6	.50	−32.4	1.07	62.2	.56	81.2	.84	[a]−37.4	[a]−9.3
Total	34.30	.....	29.44	.....	27.29	−20.4	33.61	.....	27.77	.....	25.26	−17.4	−24.8

[a] On basis of 1927 amounts for others plus thistle and serviceberry since these two species were included in others in 1925, likewise for total average 1926.

The presence of logs on cut-over areas, making the available quantity of feed per shrub and per unit much larger than it would be under other conditions, results in greater concentration of sheep on particular areas. Palatability percentages of shrub species are likewise enhanced, and this explains in part the relatively higher capacity of older cut-over areas where shrubs are more abundant.

Heavy overgrazing accompanied by damage to reproduction occurred in several areas along the railroad track and on old railroad grades as a result of the tendency of the sheep to bed on the only available open areas. Portions of the upper end of the area were only lightly used, and some small parts were entirely unused.

On Douglas fir cut-over lands within the national forests there is no intention to prolong grazing use indefinitely. On these lands changes in the herbaceous and shrub vegetation are rapid, and present conditions indicate strongly that even under the most scientific management grazing use can not be indefinitely prolonged. In other words, given protection from subsequent fires, reforestation will ultimately take place on Douglas fir cut-over lands and crowd out the palatable forage.

REDUCTION IN FIRE HAZARD

The figures (Table 5) on utilization do not accurately portray the opening up of the stand of vegetation, nor do they show the actual annual removal, due to grazing, of a considerable proportion of the highly inflammable material which otherwise would accumulate from year to year. At that, actual utilization percentage of the volume of vegetation grown (averaging for the transect 56 per cent in 1925, 52 per cent in 1926, 58 per cent in 1927, and less than 40 per cent in 1928) indicates a considerable consumption of material. Thus there is a reduction in the percentage of inflammable material. Its inflammability is reduced when it is broken up and trampled in being grazed, and particularly when the dry material is partly worked into the soil where it may absorb moisture and can not burn so readily. A comparison of views A and B in Figures 15 and 16 gives a clear picture of the usefulness of grazing in reducing hazard.

As a means of reducing fire hazard, proper utilization of Douglas fir cut-over areas consequently hinges on the principle of fullest possible grazing use up to the point where damage to forest-tree reproduction occurs. In practice this is not so simple as it sounds. Utilization of palatable vegetation annually must not be allowed to be so complete as to make possible an undue increase in or the introduction of range species less palatable but more inflammable, thus defeating one of the primary purposes for grazing these lands. The point at which utilization conflicts with forest regeneration and the symptoms of this conflict are important and as yet not fully determined phases of the study. Forage utilization alone will not tell this. Knowledge of all phases of range and livestock management, including proper seasonal use of the range and the actual management and satisfactory distribution of the livestock, are of equal importance. The area available for grazing is usually ample. How and when to use the range appears to be the chief problem.

CHANGES IN SPECIES AND GROUPS

Analysis of the increase or loss of the various species and groups during the 3-year period covered in Table 5 will be found interesting as indicative of the influence grazing may have in prolonging or

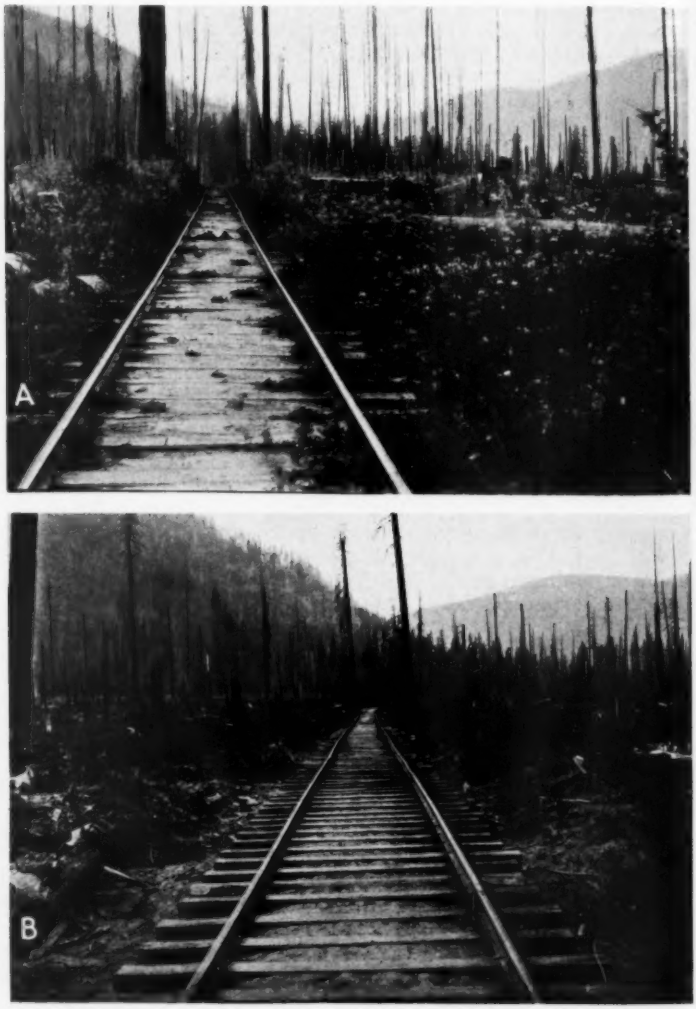

FIGURE 15.—A, Ungrazed area three years after logging; B, area shown in A after being grazed

lessening the cycle of use. Of the 24 species and groups listed on the area, 16 are of sufficient abundance, palatability, or persistence in the type to justify comment. These are fireweed, bracken, grasses and sedges, blackberry, maple, pea vine, Oregon hollygrape, rose,

lotus, willow, elder, dogwood, huckleberry, hawkweed, groundsel, and salal.

Grasses and sedges may be grouped together for the present, although later on, as they increase and become more important in the type, separation by species may be necessary. This same principle applies to plants of such genera as Linnaea, Viola, Lupinus, Vancouveria, Trientalis, Spiraea, Madia, Disporum, Anemone, Rumex, Rubus, Symphoricarpos, and Malva, which are at present found only

FIGURE 16.—A, Heavy stand of vegetation (principally fireweed) prior to grazing; B, area shown in A after heavy grazing use

rarely and are accordingly grouped as "others." Serviceberry and thistle, since on some plots they appeared to increase rapidly, were in 1926 and 1927 considered separately.

FIREWEED

Fireweed was found on all the plots and was, as previously stated, by far the most abundant. In 1925 it formed a density of 14.6 per

cent of the total ground cover on ungrazed plots and 13.0 per cent on grazed. In 1927, after two years of grazing use (utilization of fireweed averaging, on the basis of a weighted average, about 72 per cent of the foliage produced in 1925, and 56 per cent in 1926) there was a reduction of 74 per cent on grazed plots as compared to 65 per cent on ungrazed, a difference of 9 per cent. The heavy reduction on ungrazed areas would indicate that climatic, soil, and other conditions coupled with natural succession, and not the grazing factor, influenced this species most. It is rather significant, however, that on the grazed plots the greatest actual and percentage reductions occurred on those areas where grazing was heaviest, and that a relatively small change occurred in most instances when about 50 per cent or less of the foliage was grazed. On every area but one the decrease in density of fireweed was greater under grazing than under protection from grazing.

Bracken

Bracken was second in abundance, with a density in 1925 of 6.1 on grazed plots and 4.0 on ungrazed. After two years a reduction of 26 per cent occurred on the protected as compared with an increase of 20 per cent on grazed plots. Bracken is distinctly a species of low palatability. It was almost unused in 1925, many plots having no record of utilization whatever. In 1926 approximately 18 per cent of its foliage was utilized on plots showing utilization, and that mainly in its early stages of growth. Considerable trampling also occurred, however, and this together with soil disturbance and removal of competition would be expected to stimulate or at least encourage this species under grazing.

Grasses and Sedges

Grass and sedge, as a group, with a density of 2.6 on grazed and 2.6 on ungrazed plots in 1925, increased about 20 per cent on areas grazed and decreased about 11 per cent under protection, mainly on one plot, in the two years. The difference here is partly explained by the heavy grazing utilization of these plants, 84 per cent in 1925 and 99 per cent in 1926. The species present apparently were not injured by the heavy utilization by sheep. An increase in density was recorded on all the grazed areas but A. Normally this group of plants increases in the early stages of succession; the study to date appears to indicate that grazing tends to accentuate this increase.

Miscellaneous Species

Blackberry increased 19 per cent on grazed plots as compared with about 38 per cent on the ungrazed. This difference doubtless was due to the grazing and disturbance of this species. On areas A and B where blackberry was rather abundant and where the heaviest utilization prevailed considerable loss in density occurred. This was offset on the average for the whole transect by rather material increases on all but one of the other plots, on which the grazing use of blackberry was not so heavy.

Maple under grazing made no increase, although it showed a 64 per cent increase on ungrazed plots.

Pea vine, occurring only on a few plots of area B but rather abundantly there, showed about the same decline on protected and grazed

plots. This decline indicates rather the influence of unfavorable season or other growing conditions than any effect of grazing utilization of the foliage, which was complete in both years on areas available for grazing.

The decline of Oregon hollygrape was greater on ungrazed than on grazed plots (23 per cent decrease on ungrazed and only 4 per cent on grazed). Just why this hardy perennial of low palatability should decline at all is not clear, except that it needs a moderate shade which in the early stages was lacking. The only other explanation which suggests itself is that the seasons of the study period were unfavorable. The lesser decline under grazing use may possibly be due to the beneficial effect of soil disturbance. At least, it is safe to say that grazing use exerted only a negligible influence.

Of the remaining species none had sufficient density for their changes to be of special significance. It may be of interest to note that the highly palatable lotus and the slightly less palatable willow declined much more on grazed than on protected areas. The proportionately heavier increase in rose on the protected than on the grazed plots is readily explained only by the heavy use of this species by sheep. Dogwood and elder were affected in the same way. Huckleberry, on the other hand, in spite of 63 per cent utilization of its foliage in 1925 and 49 per cent in 1926, showed a greater increase on grazed areas than on protected. Although occupying a relatively small proportion of the stand, this species exhibited considerable persistence through its increase under both grazed and protected conditions. A similar reaction occurred with the highly palatable hawkweed and the moderately palatable groundsel, and also with salal, a species of low palatability. These facts, while interesting, are by no means conclusive. Succession and the effect of the several influences thereon can be determined only through further study.

POISONOUS PLANTS

As a rule in the early stages on Douglas fir cut-over lands no plants poisonous to livestock are found. This is natural in view of the rapidly transitory nature of the vegetation. Scattered rhododendron plants in the original type may survive a fire, and dogbane, an almost woody, perennial weed, also is occasionally found. These tough, leathery-leaved, and unpalatable species are seldom touched where the area is moderately grazed and other more palatable vegetation is present. On the Columbia National Forest area colonies of dogbane occur, but only one case of temporary poisoning was noted, in 1925. Around the bed ground, this plant may be nibbled by the sheep. It declined materially from 1925 to 1927 on both grazed and ungrazed areas.

EFFECT OF GRAZING ON CONIFER SEEDLINGS

The establishment and protection of conifer seedlings are prime objectives toward which proper grazing use must be directed. A brief statement of the results recorded to date may be made, although great reliance can not be placed upon their indications. Sufficient time has not elapsed to gauge properly the cumulative effect. The major difficulty thus far has been the dearth of tree-seed crops on the area under intensive study, a condition that has been general for the region as a whole during this period.

Generally speaking, except where livestock were bedded or where palatable vegetation was scarce, damage to seedlings from trampling was greater than that from nipping. Lighter utilization of vegetation usually suggests less damage. In large areas of unpalatable vegetation, trailing occurred, and seedlings were browsed to a greater extent.

Data collected in 1925 and 1926 on the grazed plots of the Wind River cut-over area in comparison with comparable inclosures brought out the interesting fact that better seedling survival (all ages) occurred, particularly in the second year, on grazed than on ungrazed plots. In 1925, 71 per cent of seedlings survived on protected plots, whereas 72 per cent survived on the grazed plots, the survival percentage varying from 52 on heavily grazed areas up to 85 on those which were moderately grazed. In 1926, the survival percentage was far in excess of that obtained on protected plots, being 86 per cent (all ages) for the moderately grazed as compared with 67 per cent for the heavily grazed, and 41 per cent for the ungrazed areas. The inclusion of plots where heavy germination and loss of hemlock occurred is largely responsible for these results. Segregation of the losses to determine the part grazing played was impossible.

L. A. Isaacs, summarizing the 1927 observations, points out that although the number of protected seedlings (30) and the total number of seedlings (249) on the entire group of 89 sample plots examined are so small as to make unsafe any attempt to determine the influence of grazing from them, the figures indicate a better survival on the fenced areas than on the grazed areas under such grazing management as was obtained on this particular area in that year. These findings indicate that if sheep are to be grazed on Douglas fir logged-off lands without direct serious loss in reproduction three precautions are necessary, namely, (1) the sheep should be handled in a way to prevent overgrazing and trampling of seedlings, (2) grazing should be deferred for one season on new portions of the area where heavy germination is taking place, and (3) only those areas should be grazed where the number of seedlings is so great that an increased loss would not result in understocking.

In view of the scarcity of seedlings and the consequent necessity for controlling conditions, two small plots were sown in April, 1928, to Douglas fir seed. These were grazed during the summer of 1928. On one plot, out of a total of 63 Douglas fir seedlings germinating in 1928, 28 died from natural causes and 7 from sheep grazing, while 28 survived. On the other plot, where 87 seedlings germinated, 25 died from natural causes, 3 were destroyed by sheep, and 59 survived. On both these plots heavy grazing use prevailed, and on the second plot the animals bedded. Although, as previously stated, it is premature for final conclusions, these results and a general study of the region seem to indicate that where grazing is moderate damage to and loss of seedlings from that source are of distinctly minor consequence, but that where overgrazing and premature use occur damage to forest seedlings may become a serious problem.

SUMMARY AND CONCLUSIONS

The importance of protecting Douglas fir cut-over lands west of the Cascades in Oregon and Washington from fire is unquestioned. As a means to this end, grazing by livestock which will keep down the

hazard through annual removal of the vegetation is being considered. In determining the grazing-management principles that will permit use of these lands without interference with reforestation, study of the changes in plant cover on cut-over lands is essential.

The most significant results of the sudden change from virgin forest to logged-over lands were found to be as follows: (1) Practical elimination of certain species found in the original forest; (2) suppression of other species due to changes in light, temperature, and moisture; (3) encroachment of vigorous outsiders never or rarely found in the virgin timber type; and (4) stimulated growth and rapid dominance (for a time at least) of species evidently held in check by the tree dominants in the original type.

The principal species on cut-over Douglas fir lands soon after cutting and broadcast slash disposal by burning are fireweed, bracken, and blackberry which come in in abundance rapidly. After a few years, shrub species become more important, and various grasses and sedges appear. Delaying the slash burn for about two years after logging or reburns results in a lower density of vegetation, a higher percentage of bracken, and a lower percentage of composition and density of the more palatable plants commonly found on cut-over areas.

Sheep graze a high percentage of foliage of many of the plants found on cut-over Douglas fir lands. In addition the sheep, in trailing, trample down much of the uneaten vegetation, break up a considerable part of the dry material on the ground, and work it partly into the soil where it can not burn so readily and where it is more apt to absorb moisture. Thus there is a reduction both in the percentage of inflammable material and in its inflammability.

There were naturally reductions in certain species and increases in others as indicated by the changes in density occurring from 1925 to 1927 on areas protected from grazing. Sheep grazing tended to cause a decrease in most of the more palatable plants, although the grasses and sedges found on the area tended to increase under grazing. On the other hand, the low-value bracken increased under grazing and decreased under protection from grazing.

While the cumulative effect of grazing use on conifer seedlings can not as yet be determined, the data obtained seem to indicate that moderate grazing use is not seriously inimical to forest regeneration and is more than compensated by the protection that it affords through reduction in fire hazard.

With a view to reducing fire hazard on cut-over Douglas fir lands, grazing utilization should involve the fullest possible grazing use that does not result in permanent damage to the range. Such utilization should not damage forest-tree reproduction or cause an undue decline in the proportion of the more palatable plants present with consequent introduction of range species of low palatability and greater inflammability.

INHERITANCE OF RESISTANCE TO RUST, PUCCINIA SORGHI, IN MAIZE[1]

By E. B. MAINS[2]

Formerly *Associate in Botany, Purdue University Agricultural Experiment Station,* and formerly *Agent, Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

Studies of *Puccinia sorhgi* Schw. were started in 1918 at La Fayette, Ind., in cooperation with the Division of Cereal Crops and Diseases. A large number of inbred lines of corn were made available for study of rust reaction,[3] and from these a number of lines of the Golden Glow, Golden Rod, and Howling Mob varieties were found to contain individuals highly resistant to the culture of rust used (*9*).[4]

Such resistant individuals were selected and inbred. From them lines have been developed that are homozygous for resistance to the rust used.

PHYSIOLOGIC FORMS OF PUCCINIA SORGHI

Further study resulted in the discovery that *Puccinia sorghi* contains a number of physiologic forms (*8*) from which some of these inbred lines differed considerably in reaction. Table 1 gives the differences in reaction shown by seedlings of five of these inbred lines during the winter months in the greenhouse. Determination of physiologic forms on these lines is best made in the months from December to April, since the rust development on resistant lines is less and the difference between resistant and susceptible lines is more pronounced than during the remainder of the year.

TABLE 1.—*Reaction of inbred lines from five selections of maize to three physiologic forms of rust, Puccinia sorghi*

Variety	Accession No.[a]	Reaction to physiologic form—[b]		
		1	3	4
Golden Bantam	995–R	0–1	3–4	4
Golden Rod	959–R	0–2	3–4	4
Howling Mob	983–R	0–1	3–4	4
Golden Glow	208–R	0–1	0–1	4
Do	202–R	0–1	0–1	4

[a] Accession number of the department of botany, Purdue University Agricultural Experiment Station. Each of these represents a group of resistant selections apparently alike for rust reaction.

[b] Designations of reactions are as follows: 0, Highly resistant, no uredinia, infection indicated by small necrotic areas or flecks; 1, very resistant, uredinia small, accompanied by necrosis, many necrotic areas without uredinia; 2, moderately resistant, uredinia of moderate size, accompanied by necrosis, necrotic areas occasionally without uredinia; 3, moderately susceptible, uredinia of moderate size, accompanied by more or less chlorosis; 4, very susceptible, uredinia well developed, little or no chlorosis.

[1] Received for publication Mar. 18, 1931; issued September, 1931. Contribution from the department of botany, Purdue University Agricultural Experiment Station and the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

[2] Now of the department of botany, University of Michigan.

[3] These lines were made available through the kindness of G. N. Hoffer, J. F. Trost, G. M. Smith, and B. H. Duddleston, who were engaged in a study of corn root rots. Other lines of corn bearing various genetic factors for use in these studies were furnished by R. A. Emerson, E. W. Lindstrom, M. Demerec, and I. F. Phipps.

[4] Reference is made by number (italic) to Literature Cited, p. 430.

From Table 1 it is to be noted that Golden Bantam 996–R (fig. 1), Golden Rod 959–R, Howling Mob 983–R (fig. 2), Golden Glow 208–R (fig. 3), and Golden Glow 202–R show pronounced resistance to physiologic form 1, while the first three lines are susceptible to physiologic form 3. Both of the Golden Glow selections, however, show pronounced resistance to physiologic form 3. (Fig. 3.) All selections are susceptible to physiologic form 4. The physiologic form previously described as 2 (*8*) is not included in this discussion, because the Ball pop corn variety, which was supposed to differentiate it from form 1, has been found to be so variable in reaction that it is

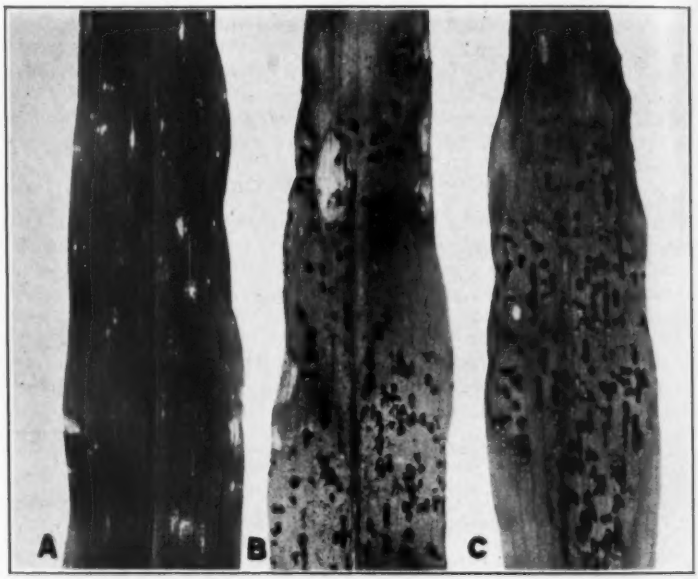

FIGURE 1.—Reaction of Golden Bantam 996–R in the seedling stage during midwinter to physiologic forms of *Puccinia sorghi:* A, To physiologic form 1 (resistant); B, to physiologic form 3 (susceptible); C, to physiologic form 4 (susceptible)

questionable whether physiologic form 2 actually is distinct from form 1. Stakman, Christensen, and Brewbaker (*10*), using eight other inbred lines, have distinguished seven physiologic forms.

INHERITANCE OF RESISTANCE

Studies of the inheritance of resistance were begun in 1924, when a number of the selections resistant to physiologic form 1 were crossed with inbred lines homozygous for susceptibility. These studies for the most part were made with the second generation and to some extent with back crosses of the first generation with the susceptible parent.

Inoculations were made on seedlings in the second-leaf to fourth-leaf stage in the greenhouse bench, mostly during the winter months. The seedlings were grown fairly close together in rows in the bench.

FIGURE 2.—Reaction of a strain of Howling Mob 983–R in the seedling stage during midwinter to three physiologic forms of *Puccinia sorghi*: A, To physiologic form 1 (resistant); B, to physiologic form 3 (susceptible); C, to physiologic form 4 (susceptible)

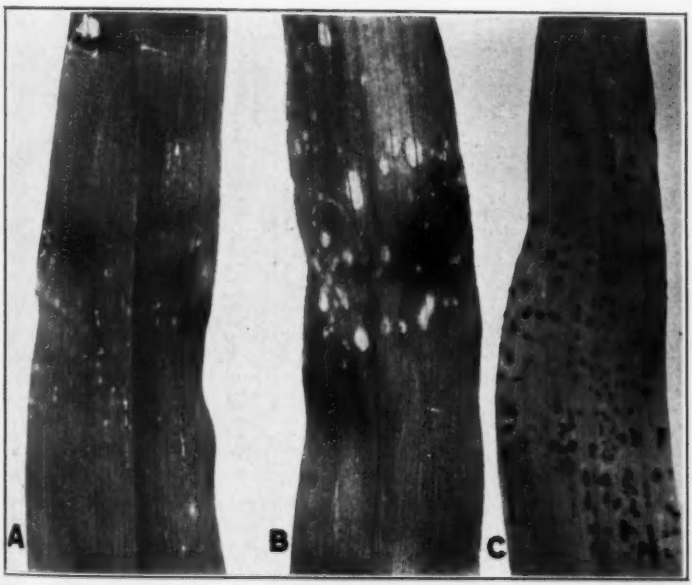

FIGURE 3.—Reaction of Golden Glow 208–R in the seedling stage during midwinter to physiologic forms of *Puccinia sorghi*: A, To physiologic form 1 (resistant); B, to physiologic form 3 (resistant); C, to physiologic form 4 (susceptible)

The stock culture of the physiologic forms of rust was maintained on a susceptible variety. Heavily rusted plants of the stock cultures were shaken over the seedlings to be tested in order to dust them with urediniospores. These plants were then atomized and maintained at high humidity by covering them overnight with wet muslin cloths. Uredinia usually appeared on susceptible individuals in about seven days. The seedlings were pulled and classified for rust reaction 10 to 14 days after inoculation.

GOLDEN GLOW 208–R SELECTIONS

Table 2 gives the results obtained in a study of hybrids between resistant strains of Golden Glow 208–R and susceptible strains of Golden Glow, Early Yellow dent, Lancaster County, Johnson County White, and Nebraska Hybrid. These were inoculated with physiologic form 1 of the rust. All the susceptible parents showed a type-4 reaction to this form, and the resistant parents were 0 to 1 in reaction. All the F_1 of these hybrids were resistant. The susceptible segregates showed a type-4 reaction. The resistant segregates had a somewhat greater range of reaction than the resistant parent, varying from 0 to 2. The difference between the two groups, however, was very marked.

TABLE 2.—*Inheritance of the resistance of Golden Glow 208–R resistant selections to physiologic form 1 of Puccinia sorghi in the F_2 of crosses and in back crosses with various susceptible lines*

Susceptible parent	Susceptible segregates	Resistant segregates	Ratio	Dev.	P. E.	Dev. / P. E.
G. G.[a] 228-1-7-1	67	204	0.989:3.011	0.75	4.81	0.15
G. G. 228-1-3-1-1	44	110	1.143:2.857	5.50	3.62	1.52
G. G. 228-1-3-1-1 Bx [b]	757	730	1.018:0.982	13.50	13.04	1.04
G. G. 228-2-5-4-5	79	257	.940:3.060	5.00	5.35	.93
G. G. 228-2-5-4-5 Bx [b]	113	157	.837:1.163	22.00	5.54	3.97
G. G. 228-3-1-3	114	334	1.018:2.982	2.00	6.18	.32
E. Y. D.[c] 51-14-3-1-3	545	1,737	.955:3.045	25.50	13.95	1.82
E. Y. D. 51-14-3-2-3	234	719	.982:3.018	4.25	9.02	.47
E. Y. D. 51-15-1-2-2	1,221	3,844	.964:3.036	45.25	20.83	2.17
E. Y. D. 51-15-1-2-2 Bx [b]	222	222	1.000:1.000	0	7.11	0
E. Y. D. 74-1-2-1-1	1,243	3,875	.971:3.029	36.50	20.94	1.74
E. Y. D. 74-1-2-1-1 Bx [b]	466	501	.964:1.036	17.50	10.49	1.67
E. Y. D. 76-10-6-1-1-1	779	2,350	.996:3.004	3.25	16.36	.19
E. Y. D. 76-10-6-1-1-1 Bx [b]	68	83	.901:1.099	7.50	4.14	1.81
E. Y. D. T188	256	694	1.078:2.922	18.50	9.00	2.06
E. Y. D. T188 Bx [b]	768	754	1.009:0.991	7.00	13.19	.53
L. C.[d] 1-1-2-4-1-2	567	1,726	.989:3.011	6.25	13.98	.44
L. C. 1-1-2-2-3-2	336	1,087	.944:3.056	19.75	10.99	1.79
L. C. 1-1-2-2-3-2 Bx [b]	473	445	1.031:0.969	14.00	10.22	1.37
L. C. 1-2-1-1-2-5	209	757	1.049:2.951	12.50	9.37	1.33
L. C. 1-2-1-1-2-5 Bx [b]	337	362	.964:1.036	12.50	8.92	1.40
L. C. 3-3-1-1-1-1	625	1,847	1.011:2.989	7.00	14.52	.48
L. C. T322	160	477	1.005:2.995	.75	7.37	.10
L. C. T322 Bx [b]	314	288	1.043:0.957	13.00	8.27	1.57
J. C. W.[e] 661	114	379	.925:3.075	9.25	6.48	1.43
J. C. W. 661 Bx [b]	665	630	1.027:0.973	17.50	12.18	1.44
N. H.[f] 377	138	392	1.042:2.958	5.50	6.72	.82
N. H. 377 Bx [b]	261	229	1.065:0.935	16.00	7.47	2.14

[a] Golden Glow.
[b] F_1 back crossed by the susceptible parent; data recorded on first generation following the back cross.
[c] Early Yellow dent.
[d] Lancaster County.
[e] Johnson County White.
[f] Nebraska Hybrid.

As shown in Table 2, the segregation in the second generation approached very closely a ratio of 3 resistant to 1 susceptible. In the back crosses of the F_1 with the susceptible parent the ratio approx-

imated 1 resistant to 1 susceptible. This would indicate that the resistance of the Golden Glow 208–R selections to physiologic form 1 of *Puccinia sorghi* depends on a simple, dominant Mendelian factor.

Since the selections of Golden Glow 208–R are also resistant to physiologic form 3, hybrids with susceptible lines of Golden Glow, Johnson County White, Early Yellow dent, and Howling Mob were studied for the inheritance of resistance to physiologic form 3. Golden Glow 208–R selections showed reactions to physiologic form 3 very similar to those shown to physiologic form 1. All the susceptible parents showed a type–4 reaction. It is interesting to note that Howling Mob is susceptible to physiologic form 3, while it is resistant to physiologic form 1. (See Tables 1 and 4.)

As shown in Table 3, the segregation in the second generation of these crosses approached very closely a ratio of 3 resistant to 1 susceptible. (Fig. 4.) The back crosses of F_1 by the susceptible parents closely approached a ratio of 1 resistant and 1 susceptible. (Fig. 4.) The resistance of Golden Glow 208–R selections to physiologic form 3 is also apparently due to a simple, dominant Mendelian factor.

TABLE 3.—*Inheritance of the resistance of Golden Glow 208–R resistant selections to physiologic form 3 of Puccinia sorhgi in the* F_2 *of crosses and in back crosses with various susceptible lines*

Susceptible parent	Susceptible segregates	Resistant segregates	Ratio	Dev.	P. E.	Dev. / P. E.
G. G. [a] 208–4–1–2–1	65	211	0.942:3.058	4.00	4.85	0.82
G. G. 208–4–1–2–1 Bx [b]	151	161	.968:1.032	5.00	5.96	.84
G. G. 228–2–4–2	197	639	.943:3.057	12.00	8.44	1.43
G. G. 228–2–4–2 Bx [b]	158	180	.935:1.065	11.00	6.20	1.77
G. G. 228–3–1–2	135	385	1.038:2.962	5.00	6.66	.75
G. G. 228–2–2–5–4	1,248	3,788	.991:3.009	11.00	20.77	.53
G. G. 228–2–2–5–4 Bx [b]	852	911	.967:1.033	29.50	14.15	2.08
J. C. W. [c] T 578	930	2,733	1.016:2.984	14.25	17.69	.81
J. C. W. T 578 Bx [b]	1,885	1,919	.991:1.009	17.00	20.81	.82
E. Y. D. [d] 51–14–3–1–3	121	352	1.023:2.977	2.75	6.35	.43
E. Y. D. 51–14–3–2–3	234	719	.982:3.018	4.25	9.02	.47
E. Y. D. 76–10–6–1–1	779	2,350	.996:3.004	3.25	16.36	.19
H. M. [e] 983–3–R4–2	771	2,244	1.023:2.977	17.25	16.05	1.07
H. M. 983–3–R4–2 Bx [b]	641	638	1.002: .998	1.50	12.10	.12
De nerec F2608	460	1,518	.930:3.070	34.50	13.01	2.65
Dwarf	853	2,563	.999:3.001	1.00	17.05	.06
Emerson 13	570	1,696	1.006:2.994	3.50	13.90	.25
Lindstrom 6177 (*10*)	690	2,143	.974:3.026	18.25	15.57	1.17
Emerson 4	264	914	.896:3.104	30.50	10.01	3.05
Emerson 4 Bx [b]	370	417	.940:1.060	23.50	9.46	2.48
Emerson 1	377	1,104	1.018:2.982	6.75	11.22	.60
Emerson 1 Bx [b]	371	359	1.016: .984	6.00	9.11	.66

[a] Golden Glow.
[b] F_1 back crossed by susceptible parent; data recorded on first generation following the back cross.
[c] Johnson County White.
[d] Early Yellow dent.
[e] Howling Mob.

In order to determine the relationship of the resistance of Golden Glow 208–R to physiologic forms 1 and 3, an experiment was conducted in which the second generation of a hybrid between Golden Glow 208–R selections and Early Yellow dent 51–14–3–1–3 was grown in pots and divided into two groups. One group was inoculated with physiologic form 1. This segregated in the ratio 117 susceptible to 404 resistant. The susceptible individuals were discarded, and the resistant individuals were inoculated with physiologic form 3. Of the 404 plants classified as resistant to physiologic form 1, only

one proved susceptible. It is probable that this escaped when inoculated with physiologic form 1. The other group of the F_2 seedlings was first inoculated with physiologic form 3. This group segregated in the ratio of 121 susceptible to 342 resistant. The susceptible individuals were discarded, and the 342 resistant plants were then inoculated with physiologic form 1. All these were resistant. The results indicate that the resistance of Golden Glow 208–R selections to physiologic form 1 and their resistance to physiologic form 3 are probably identical.

The inheritance of the resistance of Golden Glow 208–R selections to physiologic form 1 was studied in relation to two other factors also. In a cross with Early Yellow dent carrying an unlocated factor for albinism the ratio was 81 susceptible albino to 303 susceptible green

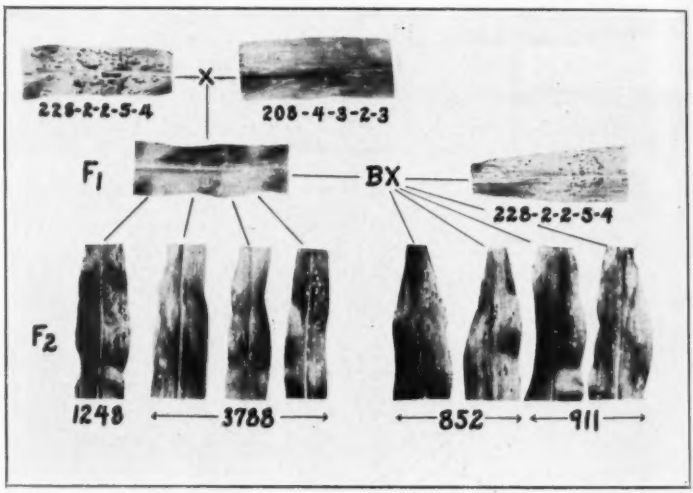

FIGURE 4.—Inheritance of resistance of Golden Glow 208–4–3–2–3 (resistant) to physiologic form 3 of *Puccinia sorghi* in the F_2 of a cross with Golden Glow 228–2–2–5–4 (susceptible) and in the back cross (Bx) of the F_1 with the susceptible parent, 228–2–2–5–4. The F_1 was resistant. The F_2 segregated in the ratio of 1,248 susceptible to 3,788 resistant (1:3), the back cross in the ratio of 852 susceptible to 911 resistant (1:1)

to 239 resistant albino to 988 resistant green. A number of the albinos died before rust developed. The expected ratio for independent inheritance would be 100.7 : 302.1 : 302.1 : 906.3.

The inheritance of resistance of Golden Glow 208–R selections to physiologic form 1 was studied in relation to tunicate ear (*1*) also. In connection with this investigation the seedlings of the F_2 were studied for reaction and classified as susceptible and resistant and were then transplanted to the field, where they were grown to maturity and classified for ear type. The ratio obtained was 25 susceptible normal to 69 susceptible tunicate to 79 resistant normal to 247 resistant tunicate, which is close to the ratio 26.2 : 78.6 : 78.6 : 235.8 expected for independent inheritance of the two pairs of factors.

The resistance of Golden Glow 208–R selections to physiologic form 3 was studied in relation to a number of other factors also.

In a hybrid with a susceptible line possessing shrunken endosperm (*7*) the F_2 gave 85 susceptible shrunken to 292 susceptible normal to 246 resistant shrunken to 858 resistant normal, which is fairly close to the ratio 92.5:277.5:277.5:832.5 expected for independent inheritance. The F_1 of this hybrid back crossed with the line bearing susceptibility and shrunken endosperm gave 177 susceptible shrunken to 194 susceptible normal to 136 resistant shrunken to 223 resistant normal, which is also fairly close to the 1:1:1:1 ratio to be expected for two pairs of independently inherited factors. In another hybrid with another susceptible line bearing shrunken endosperm the ratio in the F_2 was 88 susceptible shrunken to 372 susceptible normal to 320 resistant shrunken to 1,198 resistant normal. This approximates the calculated ratio 123.6:370.8:370.8:1,112.4 expected for independent inheritance. In both of these hybrids the shrunken classes were deficient because of the failure of a number of kernels to grow.

In a hybrid with a susceptible line bearing the tunicate-ear factor (*1*) the segregation in the F_2 was 35 susceptible normal to 102 susceptible tunicate to 81 resistant normal to 230 resistant tunicate, while the ratio calculated on the basis of independent inheritance would be 28:84:84:252.

In a hybrid with a susceptible line bearing the factor for liguleless leaf (*5*) the segregation in the F_2 was 142 susceptible liguleless to 428 susceptible ligulate to 431 resistant liguleless to 1,265 resistant ligulate, which is very close to the ratio 141.6:424.8:424.8:1,274.4 expected on the basis of independent inheritance.

In a hybrid between Johnson County White, bearing factors for susceptibility and white endosperm, and resistant Golden Glow having yellow endosperm (*4*), the ratio in F_2 was 232 susceptible white to 698 susceptible yellow to 709 resistant white to 2,034 resistant yellow, which is very close to the ratio 229.6:688.8:688.8:2,066.4 expected on the basis of independent inheritance. Back crosses of the F_1 with the susceptible white parent also gave a ratio of 956 susceptible white to 893 susceptible yellow to 968 resistant white to 933 resistant yellow, which also is close to the expected 1:1:1:1 ratio.

The inheritance of endosperm color was studied in another hybrid also, in which the ratio in the F_2 was 237 susceptible white to 616 susceptible yellow to 662 resistant white to 1,901 resistant yellow, which is close to the expected ratio 213.5:640.5:640.5:1,921.5.

The inheritance in relation to virescent seedling V_3 (*2*) was studied in hybrids with a susceptible line carrying the virescent character in a heterozygous condition. As a result only a portion of the crosses received this factor. Those in the F_2 gave a ratio of 73 susceptible virescent to 191 susceptible green to 257 resistant virescent to 657 resistant green. On the basis of independent inheritance the ratio should be 73.6:220.8:220.8:662.4. Two F_1 plants containing the virescent factor were back crossed with the susceptible parent, which was heterozygous for virescence. The ratio obtained was 96 susceptible virescent to 274 susceptible green to 116 resistant virescent to 301 resistant green. The ratio on the basis of independent inheritance should be 98.3:294.9:98.3:294.9.

The inheritance of resistance to physiologic form 3 was studied in relation to dwarf (*6*) in a hybrid with a dwarf susceptible line. In the F_2 a ratio of 306 susceptible dwarf to 1,025 susceptible tall to 950

resistant dwarf to 3,127 resistant tall was obtained. The expected ratio on the basis of independent inheritance would be 338:1,014:1,014:3,042.

GOLDEN GLOW 202–R SELECTIONS

Selections from Golden Glow 202–R showed reactions similar to those of Golden Glow 208–R to the various physiologic forms of *Puccinia sorghi*. (Table 1.) These have been studied in a number of crosses with susceptible lines. As shown in Table 4, the segregations in these crosses and back crosses approach very closely the ratios expected for a simple dominant factor.

TABLE 4.—*Inheritance of the resistance of Golden Glow 202–R resistant selections to physiologic form 3 of Puccinia sorghi in the F_2 of crosses and in back crosses with susceptible lines*

Susceptible parent	Susceptible segregates	Resistant segregates	Ratio	Dev.	P. E.	Dev./P. E.
G. G.[a] 228-2-2-2	140	456	0.940 : 3.060	9.00	7.13	1.26
G. G. 228-2-2-2 Bx [b]	313	370	.917 : 1.083	28.50	8.81	3.23
L. C.[c] 1-2-1-1-2-5	904	2,763	.986 : 3.014	12.75	17.70	.72
L. C. 1-2-1-1-2-5 Bx [b]	984	1,022	.981 : 1.019	19.00	15.12	1.26
L. C. 1-1-2-4-1-2	371	1,172	.962 : 3.038	14.75	11.47	1.29
L. C. 3-3-1-1-1-1	601	1,730	1.031 : 2.969	18.25	14.09	1.30
Phipps 2 [d]	239	776	.942 : 3.058	14.75	9.36	1.58
H. M.[e] 983-3-R4-2	781	2,244	1.033 : 2.967	24.75	16.08	1.54
H. M. 983-3-R4-2 Bx [b]	641	638	1.002 : 0.998	1.50	12.10	.12

[a] Golden Glow.
[b] F_1 back crossed by susceptible parent; data recorded on first generation following the back cross.
[c] Lancaster County.
[d] Line received from J. F. Phipps.
[e] Howling Mob.

To determine the relationship of the resistance of Golden Glow 208–R selections and Golden Glow 202–R selections, eight hybrids were made between various selections of these two strains. The F_2 of these crosses was studied for reaction to physiologic form 3. Of the 1,756 seedlings studied, none was susceptible. All proved to be markedly resistant, indicating that the resistance of the selections from Golden Glow 208–R and that of the selections from Golden Glow 202–R are probably due to the same factor.

The inheritance of the resistance of Golden Glow 202–R selections to physiologic form 3 was studied in relation to albinism, W_{11} (*3*). The hybrid was made with a susceptible line heterozygous for the albino factor, and consequently only a portion of the F_1 plants contained the factor. In the F_2 most of the albino plants died before the incubation period was over. However, in the remaining group of green seedlings, the segregation was 142 susceptible to 409 resistant, which is very close to the ratio 137.7:413.1 expected in the case of independent inheritance.

The inheritance of resistance in relation to endosperm texture (*4*) was studied in hybrids with a susceptible sweet corn, Howling Mob 983–R. The ratio in the F_2 was 181 susceptible sweet to 567 susceptible starchy to 567 resistant sweet to 1,701 resistant starchy, which approximates the calculated 189:567:567:1,701 on the basis of independent inheritance. Back crosses of the F_1 by the susceptible sweet parent gave 296 susceptible sweet to 345 susceptible starchy

to 298 resistant sweet to 340 resistant starchy. The expected ratio would be 319.7:319.7:319.7:319.7.

The inheritance of resistance to physiologic form 3 in relation to virescent seedling V_4 (*2*) was studied in hybrids with a susceptible line producing virescent seedling. The segregation in the F_2 was 61 susceptible virescent to 178 susceptible green to 210 resistant virescent to 566 resistant green. The expected ratio on the basis of independent inheritance would be 63.4:190.2:190.2:570.6.

The inheritance of resistance to physiologic form 3 in relation to liguleless leaf (*5*) was studied in a hybrid with a susceptible line carrying the liguleless factor. The F_2 gave a ratio of 53 susceptible liguleless to 186 susceptible ligulate to 214 resistant liguleless to 562 resistant ligulate, which is close to the ratio 63.4:190.2:190.2:570.6, calculated on the basis of independent inheritance.

The inheritance of resistance to physiologic form 3 in relation to endosperm color (*4*) was studied in a hybrid with a susceptible white endosperm line. The ratio in the F_2 was 157 susceptible white to 545 susceptible yellow to 600 resistant white to 1,663 resistant yellow. The expected ratio on the basis of independent inheritance would be 185.3:555.9:555.9:1,667.7. When the F_1 was back crossed with the susceptible white endosperm parent, a ratio of 321 susceptible white to 320 susceptible yellow to 307 resistant white to 331 resistant yellow was obtained, which approximates the ratio 319.7:319.7:319.7:319.7 expected in cases of independent inheritance.

HOWLING MOB 983–R SELECTIONS

As shown in Table 1, various selections of Howling Mob 983–R have shown marked resistance to physiologic form 1. The results obtained in a study of the inheritance of this resistance in crosses with susceptible lines are shown in Table 5. The classes in the F_2 were very distinct, especially during the winter months. The resistant class showed only slightly more variation than the resistant parent, and the susceptible class was very susceptible. From Table 5, it is evident that the resistance of Howling Mob 983–R selections to physiologic form 1 is inherited as a simple dominant factor.

TABLE 5.—*Inheritance of the resistance of Howling Mob 983–R resistant selections to physiologic form 1 of Puccinia sorghi in the F_2 of crosses and in back crosses with susceptible lines*

Susceptible parent	Susceptible segregates	Resistant segregates	Ratio	Dev.	P. E.	Dev. / P. E.
C. G.[a] 4-1-2-4-2	255	762	1.003:2.997	0.75	9.31	0.08
Squaw Flint	147	494	.917:3.083	13.25	7.39	1.79
E. Y. D.[b] 76-10-6-1-2-2	1,111	3,525	.959:3.041	48.00	19.87	2.41
Dwarf	331	1,032	.971:3.029	9.75	10.75	.90
Dwarf Bx[c]	110	104	1.028: .972	3.00	4.93	.61

[a] Country Gentleman.
[b] Early Yellow dent.
[c] F_1 back crossed by susceptible parent; data recorded on first generation following the back cross.

The inheritance of resistance of Howling Mob 983–R resistant selections (resistant sweet) (*4*) to physiologic form 1 was studied in relation to endosperm texture in a hybrid with Early Yellow dent (susceptible starchy). The ratio in the F_2 was 271 susceptible sweet

to 840 susceptible starchy to 870 resistant sweet to 2,655 resistant starchy. On the basis of independent inheritance this should be 289.7: 869.1: 869.1: 2,607.3.

The inheritance of resistance of Howling Mob 983–R (resistant white) to physiologic form 1 in relation to endosperm color (*4*) was studied in the hybrid with Early Yellow dent (susceptible yellow). The ratio in the F_2 was 244 susceptible white to 739 susceptible yellow to 749 resistant white to 2,320 resistant yellow. On the basis of independent inheritance this should be 253.3:759.7:759.7:2,279.3.

The inheritance of the resistance of Howling Mob 983–R (resistant tall) to physiologic form 1 was studied in relation to dwarf in a hybrid with a susceptible line carrying the dwarf factor (*6*). The F_2 gave the ratio of 94 susceptible dwarf to 237 susceptible tall to 267 resistant dwarf to 765 resistant tall. The expected ratio on the basis of independent inheritance should be 85.2:255.5:255.5:766.6. A back cross of the F_1 by the susceptible dwarf parent gave 53 susceptible dwarf to 57 susceptible tall to 48 resistant dwarf to 56 resistant tall. The expected ratio should be 53.5:53.5:53.5:53.5.

GOLDEN BANTAM 996–R SELECTIONS

Golden Bantam 996–R resistant selections also have shown marked resistance to physiologic form 1, as shown in Table 1. During the winter months these selections usually show a peculiar netted chlorosis with only occasional small uredinia. The inheritance of this resistance was studied in four hybrids. (Table 6.) The results obtained also indicate that the resistance of these selections of Golden Bantam 996–R is inherited as a simple dominant factor.

TABLE 6.—*Inheritance of the resistance of Golden Bantam 996–R resistant selections to physiologic form 1 of Puccinia sorghi in the F_2 of crosses and in back crosses with susceptible lines*

Susceptible parent	Susceptible segregates	Resistant segregates	Ratio	Dev.	P. E.	Dev. / P. E.
G. B.[a] 16	125	406	0.942:3.058	7.75	6.73	1.15
E. Y. D.[b] 76-10-6-1-2-F1	517	1,488	1.031:2.969	15.75	13.12	1.20
Dwarf	466	1,361	1.020:2.980	9.25	12.48	.74
Dwarf Bx [c]	228	227	1.002: .998	.50	7.19	.07
Emerson 12	498	1,609	.945:3.055	28.75	13.42	2.14

[a] Golden Bantam.
[b] Early Yellow dent.
[c] F_1 back crossed by susceptible parent; data recorded on first generation following the back cross.

The resistance of Golden Bantam 996–R selections (resistant sweet) to physiologic form 1 was studied in relation to a susceptible line having starchy endosperm (*4*). A ratio of 118 susceptible sweet to 348 susceptible starchy to 332 resistant sweet to 1,029 resistant starchy was obtained in the F_2. This is very close to the ratio 114.2: 342.6:342.6:1,027.8 expected on the basis of independent inheritance. In another hybrid with Early Yellow dent (susceptible starchy) the ratio in the F_2 was 61 susceptible sweet to 159 susceptible starchy to 170 resistant sweet to 481 resistant starchy. The expected ratio on the basis of independent inheritance would be 54.4:163.3:163.3:489.9.

The resistance of Golden Bantam 996–R (resistant ligulate), when studied in a susceptible line carrying the liguleless leaf factor (*5*), gave the ratio 112 susceptible liguleless to 386 susceptible ligulate to 390 resistant liguleless to 1,219 resistant ligulate in the F_2. The expected ratio on the basis of independent inheritance would be 131.7:395.1:395.1:1,185.3.

The inheritance of resistance and endosperm color (*4*) was studied in a hybrid between Golden Bantam 996–R (resistant yellow) with a susceptible line having white endosperm. The ratio obtained in the F_2 was 116 susceptible white to 346 susceptible yellow to 333 resistant white to 1,028 resistant yellow. The ratio calculated on the basis of independent inheritance would be 114:342:342:1,026.

In a hybrid with a susceptible line carrying the virescent seedling factor V_3 (*2*), a ratio of 48 susceptible virescent to 232 susceptible green to 203 resistant virescent to 651 resistant green was obtained. The expected would be 70.9:212.7:212.7:638.1. In this hybrid a number of the virescent seedlings died before the incubation period was over.

The inheritance of the resistance of Golden Bantam 996–R (tall) was studied in a hybrid with a susceptible line carrying the dwarf factor (*6*). A ratio of 119 susceptible dwarf to 347 susceptible tall to 300 resistant dwarf to 1,062 resistant tall was obtained in the F_2. The expected ratio on the basis of independent inheritance would be 114.2:342.7:342.7:1,028.2. In back crosses of the F_1 by the susceptible dwarf parent a ratio of 119 susceptible dwarf to 109 susceptible tall to 113 resistant dwarf to 114 resistant tall was obtained. This is very close to the expected ratio of 113.7:113.7:113.7:113.7.

All the resistant selections of Golden Bantam, Howling Mob, and Golden Glow thus far studied have been remarkable for their simple and clear-cut inheritance of resistance. Under greenhouse conditions that favored the greatest expression of resistance, such as the lower light intensities and lower temperatures of winter months, there was a very sharp separation into two distinct classes in the seedling stage. Under conditions more favorable to the development of the rust, such as high light intensities and temperatures, there was a tendency for many individuals in the resistant group to produce more uredinia. Such individuals, however, could be easily distinguished from those of the susceptible group by their fewer and smaller uredinia and by the marked necrosis accompanying infection.

The reaction to rust is as sharply inherited as are many morphological characters, such as albinism, endosperm color, texture, etc. In nearly all cases the segregation in the F_2 is in the ratio of 3 resistant to 1 susceptible. When the F_1 was back crossed with the susceptible parent the ratio was 1 resistant to 1 susceptible, as would be expected for the inheritance of a single simple factor.

The foregoing results indicate that the rust resistance of these selections is specially suitable for a study of linkage. So far, however, no evidence of linkage has been obtained in studies involving endosperm texture and color, dwarfness, albinism (W_{11}), virescent seedling (V_3, V_4), liguleless leaf, tunicate ear, or shrunken endosperm.

The uniformity of resistance in hybrids between selections of Golden Glow 208–R and Golden Glow 202–R indicates that the resistance of these two groups of selections is due to the same factor. Apparently the same factor is responsible for the resistance to physio-

logic forms 1 and 3 also, since selections resistant to one form are resistant to the other. The resistance of these selections, therefore, is probably due to a different factor from that responsible for the resistance of the selections of Golden Bantam 996–R and Howling Mob 983–R, for the latter are resistant only to physiologic form 1. This difference has not been checked genetically, nor has the relationship of the resistance of the resistant Golden Bantam and Howling Mob been determined.

SUMMARY

Selections from Golden Glow 208–R and Golden Glow 202–R have been found to be highly resistant to physiologic forms 1 and 3 of *Puccinia sorghi*.

When these selections were crossed with susceptible selections, this resistance was found to be inherited in a very definite manner, the segregation in the F_2 being 3 resistant to 1 susceptible. When the F_1 of such crosses was back crossed with the susceptible parents, the ratio obtained was 1 resistant to 1 susceptible. This indicates that the resistance of these selections to physiologic forms 1 and 3 depends on a simple Mendelian factor.

Selections from Golden Bantam 996–R and Howling Mob 983–R have shown resistance only to physiologic form 1 of *Puccinia sorghi*.

When these selections were crossed with susceptible selections, the resistance to physiologic form 1 was inherited in a ratio of 3 resistant to 1 susceptible. Back crosses of the F_1 by the susceptible parents gave a ratio of 1 resistant to 1 susceptible, indicating that their resistance to physiologic form 1 is likewise due to a simple Mendelian factor.

In studies thus far made no case of linkage of rust resistance with other factors has been noted.

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A CYTOSPORA CANKER OF APPLE TREES[1]

By D. F. FISHER, *Principal Horticulturist*, and E. L. REEVES, *Junior Pathologist*, *Division of Horticultural Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

Some 200 species of Cytospora have been described, but most of them are recognized as saprophytes. The only serious tree disease in the United States known to be due to Cytospora occurs on poplars and willows and is caused by *C. chrysosperma*.[2]

A Cytospora variously assigned to the species *rubescens*, *ambiens*, or *leucostoma* has been reported from widely separated parts of the world as causing a die-back of fruit trees, particularly stone fruits. In the United States the occurrence of a Cytospora canker on apples was first reported from Illinois by Stevens.[3] He described the disease from observation of a single canker taken from a young tree that had died.

Leonian [4] found a Valsa canker together with its Cytospora stage to be common on apple trees in New Mexico. He conducted inoculation experiments and concluded that the fungus, which he accepted as *Cytospora leucostoma*, is a weak wound parasite only. He obtained cankers from inoculations on weakened trees but in all cases failed to obtain any positive results from similar inoculations on healthy trees.

In the Pacific Northwest, *Cytospora* sp. is one of the most common fungi found on the dead wood of apple trees. Injury from freezing, fire, or girdling by rodents, pear blight, or other cause often kills branches and trees or so weakens them that they soon die. On such wood Cytospora commonly becomes established within a very short time. (Fig. 1.) However, it appears that the fungus is incapable of making a primary invasion of sound healthy trees, and doubt as to its ability to spread into living apple-tree tissue has always existed.

CYTOSPORA CAUSING AN ORCHARD DISEASE

About the middle of April, 1928, the attention of the writers was called to an epidemic of cankers appearing on 1-year-old Northern Spy apple trees in an orchard at Orondo, Wash. A careful examination of the orchard disclosed similar conditions on older trees of a number of varieties.

At first the bark of affected areas was darker in color and had a water-soaked appearance, but later it developed concentric zones of tan and dark brown and became slightly sunken. In a few cases the crotch tissues were affected in a manner suggestive of winter injury,

[1] Received for publication Mar. 25, 1931; issued September, 1931.

[2] LONG, W. H. AN UNDESCRIBED CANKER OF POPLARS AND WILLOWS CAUSED BY CYTOSPORA CHRYSOSPERMA. Jour. Agr. Research 13: 331-344, illus. 1918.

[3] STEVENS, F. L. AN APPLE CANKER DUE TO CYTOSPORA. Ill. Agr. Expt. Sta. Bul. 217, p. 367-379, illus. 1919.

[4] LEONIAN, L. H. STUDIES ON THE VALSA APPLE CANKER IN NEW MEXICO. Phytopathology 11: 236-243. 1921.

and in the ordinary course of events the occurrence would have been explained on that basis. However, identical-appearing injuries were found around the buds near the base of the previous year's wood growth. (Fig. 2.) In other cases cankers occurred at various points not associated with buds or crotches, on growth from 1 to 3 years old. Many small branches were girdled (fig. 3), and a few of the 1-year-old Northern Spy trees were also girdled. Some of the cankers at leaf buds were as small as one-eighth inch in diameter, but the larger ones were 3 to 4 inches in diameter.

The section of the orchard that was most severely affected had very sandy soil, deficient in humus and underlain with gravel. This soil was easily leached and difficult to keep adequately irrigated. It had suffered from drought during the 1928 growing season, and doubtless the vitality of the trees was reduced in consequence. Whether the

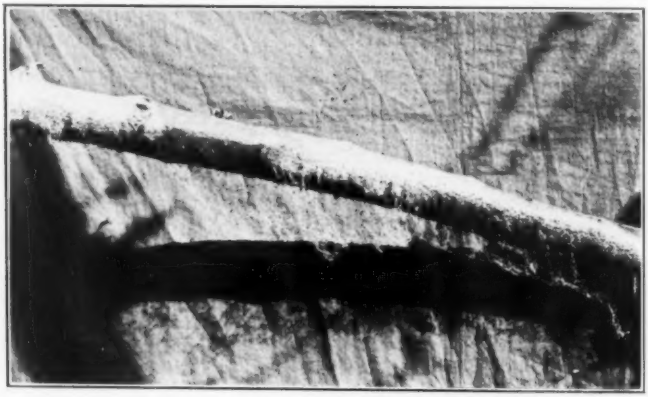

FIGURE 1.—Cytospora fruiting on an apple branch killed by fire. Orondo, Wash.

affected areas had been injured primarily by freezing could not be determined at the time they were first observed, but Cytospora was readily isolated from such injured areas. The fungus was found not only in the older portions of the cankers but also actively invading surrounding bark tissue which showed no injury.

Enlargement of the cankers continued until the latter part of May, when the affected areas began to be delimited. The dead tissues cracked away from the margins of the cankers, and callus formation proceeded. On June 6 numerous pycnidia appeared in the cankered bark and characteristic orange-colored spore masses were found pushing out like tendrils from them.

During the 1928 growing season the orchard received excellent care and attention. The trees were fertilized and an abundant supply of irrigation water was provided at all times. As a result a very good growth was secured, and a terminal extension of from 24 to 30 inches was not uncommon even on the older trees. The cankers ceased to enlarge after about June 1, and even the untreated dead areas began to heal, as well as those that had received surgical attention. No further enlargement of any of the cankers was noted either

in the 1928 growing season or during subsequent years, and eventually all of the dead areas healed over completely. (Fig. 4.)

During the summer of 1929 an even more serious manifestation of Cytospora canker on apple trees came under the writers' observation

FIGURE 2.—Cytospora cankers at base of spurs and lateral buds on Delicious apple. Orondo, Wash.

in an orchard at Columbia Gardens, British Columbia. The trees were of the Wealthy variety and about 20 years old. The branches were covered with numerous dead spots of various sizes but usually not

over one-half inch in diameter, upon which Cytospora was fruiting. The early stages of these cankers were not seen, but the fungus appeared to be the same one that had been found at Orondo, Wash. The circumstances surrounding its occurrence at Columbia Gardens were almost parallel to those that had prevailed at Orondo. The soil

FIGURE 3.—Girdling of small branches by Cytospora on Northern Spy apple. Orondo, Wash.

is very sandy and open and lacking in organic matter like most of the lower bench lands along the Columbia River. Irrigation was entirely inadequate, and there was abundant evidence of general winter injury, together with damage from smelter fumes, with consequent reduced vitality of the trees.

EXPERIMENTAL WORK

TREE SURGERY

A number of experiments were conducted on the control of the disease, principally by surgical methods. As soon as the disease was discovered in April, 1928, some of the badly cankered young Northern Spy trees were cut off close to the ground and new tops were allowed to develop. On others the cankers were cut out with a knife and the wounds were then treated with a disinfectant paint. On older trees badly cankered branches were pruned off and the remaining cankers were chiseled out to sound tissue all around and

FIGURE 4.—Northern Spy apple tree with cankers on the trunk which received surgical treatment. Healing was hastened by the use of an asphaltum wound dressing. Orondo, Wash.

then treated with disinfectant paints. Other cankers were excised in the same manner but received no disinfectant or wound dressing of any kind. Untreated cankers were retained as checks. No marked difference in results was noted among the several treatments except as noted below, and, as already indicated, the untreated cankers ceased enlarging about June 1, eventually healing over as well as those that received surgical treatment.

WOUND DRESSINGS

Observations were made on the effects of various wound dressings. These materials included (1) a commercial preparation containing 1 per cent copper in a fish-oil soap mixture, (2) a Bordeaux paint made

by mixing commercial powdered Bordeaux mixture (containing about 10 per cent copper) with sufficient raw linseed oil to make a thick paint, and (3) asphaltum roofing paint of a consistency permitting cold application with an ordinary paint brush. Cankers treated with the asphaltum healed a little more rapidly than checks and showed no toxic effect from the paint. (Fig. 4.) There was evidence of slight toxic effect from the Bordeaux paint, especially on the yearling trees. Callus formation was somewhat retarded by it (fig. 5), and the leaves growing beyond the treated cankers often showed burned margins, indicating that toxic materials had been transported in the sap stream. No injury followed application of the copper soap, but healing of the wounds was not as rapid as in cases where asphaltum was used.

DISINFECTION WITHOUT CUTTING

In other experiments strong and penetrating disinfectants were applied without any surgical work. An alcoholic solution of zinc chloride such as is used for pear blight in California [5] and a mixture of sodium arsenite and raw linseed oil were used. Care was taken not to apply either material much beyond the limits of the canker, but in all cases, with both materials, adjacent bark and wood were injured and rather severe foliage injury occurred, indicating that in this case also toxic substances had been introduced into the sap stream.

FIGURE 5.—Northern Spy apple tree with cankers that received surgical treatment and Bordeaux paint. Healing was somewhat retarded, and a toxic effect was also noted in the leaves

ARTIFICIAL INOCULATIONS

In order to test the pathogenicity of Cytospora on apple wood, a large number of artificial inoculations were made during the late winter and early spring of 1930 in an orchard near Wenatchee, Wash. Inoculum was obtained from fresh isolations of the Cytospora commonly found fruiting on apple wood near Orondo, Wash. Spores from pure cultures as well as those taken directly from fruiting cankers were used. Inoculations were made by atomizing spore suspensions on (1) the basal portion of the previous year's growth, such as had been found to be commonly infected at Orondo in 1928; (2) old pruning cuts; and (3) fresh pruning cuts and other injuries made in sound wood of various ages. In addition to the inoculations on healthy trees, a series of similar inoculations was made on trees that had suffered freezing injury from the extreme cold of the previous winter.

[5] DAY, L. H. ZINC CHLORIDE TREATMENT FOR PEAR BLIGHT CANKERS. Calif. Agr. Col. Ext. Circ. 45, 13 p. 1930.

Observations were continued periodically until the middle of July, 1930, but in no case did infection occur.

DISCUSSION

The occurrence of the fungus as a facultative parasite both at Orondo, Wash., and at Columbia Gardens, British Columbia, was associated with conditions of reduced vitality of the trees. The open sandy soil upon which the orchards were located in both places could not support a vigorous tree growth in the absence of irrigation and fertilization.

It is well known that basal buds normally produce less vigorous leaf or shoot growth than apical buds or buds located near the end of the shoot. It is a fact also that in the irrigated regions of the Pacific Northwest the buds on the lower portion of apple shoots sometimes do not "break" and leaves are produced only on the terminal portion. An exaggerated development of this is seen in the trouble known as rosette. Under severe drought conditions it is probable that the weak buds on the basal portion of the shoots may be arrested in their development and die either as a result of the drought itself or from freezing injury during the ensuing winter. On such dead tissue Cytospora would have little difficulty in becoming established, and presumably might grow into adjacent dead or weakened woody tissue to form the small cankers observed in the cases described.

Killing of bark tissues in the crotch region is one of the most common manifestations of freezing injury on fruit trees. The subsequent infection of such areas by Cytospora has also been observed very frequently, so that the occurrence of these cankerous areas yielding the fungus in the case described may be accounted for in this way.

The explanation of the disease as outlined above is supported by the fact that its disappearance, even without surgical or other treatment, in the orchard at Orondo, Wash., was coincident with the reestablishment of normal tree growth and vigor. The failure of all attempts to inoculate healthy growing parts, or even those that had been weakened but not entirely killed by winter injury, adds convincing proof of the essentially nonparasitic character of the organism being studied.

SUMMARY

An epidemic of cankers caused by Cytospora on apple trees at Orondo, Wash., is described.

Surgical treatment was given the cankers, and a number of disinfectant wound dressings were tested. Toxic effects on foliage were noted following the use of copper paint on the canker, indicating that injurious materials were introduced into the sap stream. Copper soap did not prove to be toxic, but wounds treated with it did not heal as rapidly as where asphaltum paint was used. Where asphaltum paint was used healing appeared to be hastened and no toxic effects were observed.

Strong and penetrating disinfectants were used on cankers which received no surgical treatment. Injurious effects were produced in all cases, not only in bark and wood tissues but in the foliage as well. The materials tested were (1) alcoholic solutions of zinc chloride such as are sometimes employed for pear blight and (2) a mixture of sodium arsenite and linseed oil.

Artificial inoculations produced negative results on sound apple wood and also on wood which had been winter injured but not killed.

It is concluded that under normal conditions Cytospora is not parasitic on apple wood. In the epidemic studied the fungus probably became established on dead parts and later was able to make some progress into adjacent tissue weakened and devitalized as a result of poor growing conditions during the preceding season. With the restoration of good cultural conditions and normal growth the enlargement of cankers ceased and the affected areas healed over completely. This occurred in the case of check cankers as well as those that received surgical treatment.

DURATION OF THE FLOWERLESS CONDITION OF SOME PLANTS IN RESPONSE TO UNFAVORABLE LENGTHS OF DAY[1]

By W. W. GARNER, *Principal Physiologist in Charge*, and H. A. ALLARD, *Senior Physiologist, Division of Tobacco and Plant Nutrition, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

Plants which attain their most successful floriferous expression on an increasing length of day have been termed long-day types of plants. Plants which attain flowering on a decreasing length of day have been termed short-day types. Where flowering is the rule whether the days are long or short, other conditions being equal, it has been convenient to think of them as plants of indeterminate flowering habit.

In any latitude north or south of the equatorial regions the longest days occur at the midsummer period. A strictly long-day type of plant for this latitude flowers in response to the midsummer length of day and ceases flowering when the seasonal length of day has sufficiently shortened in autumn. It is evident that a long-day type of plant can flower only when the midsummer length of day is long enough to promote flowering.

Considerable experimental evidence has been secured bearing on the relation of the flowering behavior of certain long-day perennial types to favorable lengths of day. Many perennial plants flower in the Washington latitude in response to the longest midsummer days but can not flower when the days have reached 12 hours or less in length. The winter behavior of such plants is characteristically one of more or less complete dormancy of the vegetative parts, or even in some cases of death of the aboveground stems, even when the plants are grown under optimum conditions of temperature in the greenhouse.

It is of some interest to know how long a herbaceous plant can be maintained in a flowerless, growing condition by a suitable length of day. Either short-day or long-day types of plants can be made the subject of experimentation. However, in the case of the short-day type of plants, artificial illumination is required to prevent the effects of a shortening autumnal length of day, which would normally result in flowering and perhaps ultimate senility. Owing to problems involving intensity and quality of illumination and other conditions incident to the use of artificial light, experimentation with short-day plants becomes a matter of some difficulty. The long-day plants lend themselves more readily to favorable treatment, since this becomes a mere matter of cutting off each day the normal daylight in the early morning or late afternoon by means of dark houses until the short-length days arrive.

[1] Received for publication Mar. 24, 1931; issued September, 1931.

EXPERIMENTAL WORK

Two species of Sedum, namely, *S. woodwardii* N. E. Br. and the common garden ornamental *S. spectabile* Bor., were used in the writers' experiments. In addition to these wild senna (*Cassia marilandica* L.), a native wild species in the Washington region, has been found to be a convenient plant for such tests.

The conditions of experimentation were simple, the plants being grown in suitable containers, either boxes or pails, and placed on trucks which were run into ventilated dark houses at a certain time each afternoon, and returned to the daylight the next day on a fixed schedule. Since these plants are hardy perennials, they were left out of doors throughout the winter, and the tests were begun in March or early April before the longer days of the springtime had been experienced.

The schedule of exposures was as follows:

8-hour day, darkened 3.30 p. m. to 7.30 a. m.
10-hour day, darkened 3.30 p. m. to 5.30 a. m.
12-hour day, darkened 5.30 p. m. to 5.30 a. m.

When crowding became evident in the containers, division of the clumps was made to maintain normal growing conditions for the plants.

SEDUM WOODWARDII [1]

Experiments were begun with *Sedum woodwardii* in 1923 and continued through the season of 1930 under day lengths of 8, 10, and 12 hours. In addition, controls experiencing the full length of day were maintained.

Throughout the entire period from 1923 to 1930, inclusive, embracing a duration of eight years, all exposures of 12 hours or less each day from March until October prevented flowering, the plants remaining in a healthy, vegetative condition. The controls exposed to the full length of day flowered each summer as follows: 1923, July 7; 1924, not recorded; 1925, June 6; 1926, June 12; 1927, June 18; 1928, June 14; 1929, August 5; 1930, July 7.

SEDUM SPECTABILE

Experiments with *Sedum spectabile* were begun in 1923, the plants being maintained under day lengths of 8, 10, and 12 hours, and the full summer length of day. Growth and stem elongation were favored by all lengths of day, but flowering was completely inhibited during the period of nine years from 1921 to 1929, inclusive, except in the controls. (Fig. 1.) The controls flowered as follows: 1921, not recorded; 1922, not recorded; 1923, September 12; 1924, September 8; 1925, not recorded; 1926, September 2; 1927, September 10; 1928, August 31; 1929, September 3.

During the season of 1930 the plants that had been grown since 1921 under 10-hour-day conditions without indications of flowering were exposed to the full length of day beginning June 17. These flowered August 25, showing no delay over the controls flowering August 26, which had experienced the full length of the summer day from year to year. (Fig. 2.)

[1] Lack of comparative material leaves the exact identification of this species somewhat open. It is provisionally classified as *Sedum woodwardii* N. E. Br.

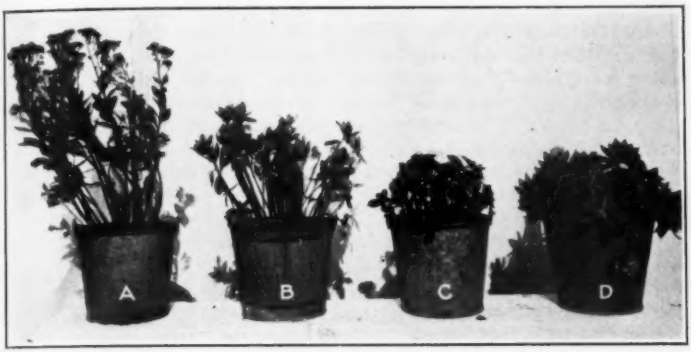

FIGURE 1.—*Sedum spectabile:* A, Control plants, which experienced the full length of day and flowered September 8; B, C, and D, plants given, respectively, 12, 10, and 8 hours of daylight each day and never able to flower. The 12-hour plants are characterized by vigorous stem growth. From 1921 to 1924, when photographed, all were grown under their respective day-length conditions each season. The controls flowered each year

FIGURE 2.—*Sedum spectabile,* a strain flowering only in response to long summer days: A, Controls, which have flowered each year since the tests were begun in 1921; B, plants given 10 hours of daylight throughout the growing season each year since 1921 and which had never flowered up to 1929. In 1930 these plants were exposed to the full length of day and flowered normally after remaining nine years in a flowerless condition

CASSIA MARILANDICA

Plants of wild senna, *Cassia marilandica*, grown from seed, have been maintained under 10-hour-day conditions from 1922 to 1930, inclusive, a period of nine years, with no indications of flowering. Under short-day conditions the plants make little growth, throwing up very weak slender stems, which remain in a half dormant condition throughout the summer, ultimately shedding their leaves and dying to the ground as in winter, much in advance of the more vigorous, flower-producing controls. (Fig. 3.)

The plants experiencing the full summer day flowered consistently each year. So far as records were made, the following flowering dates

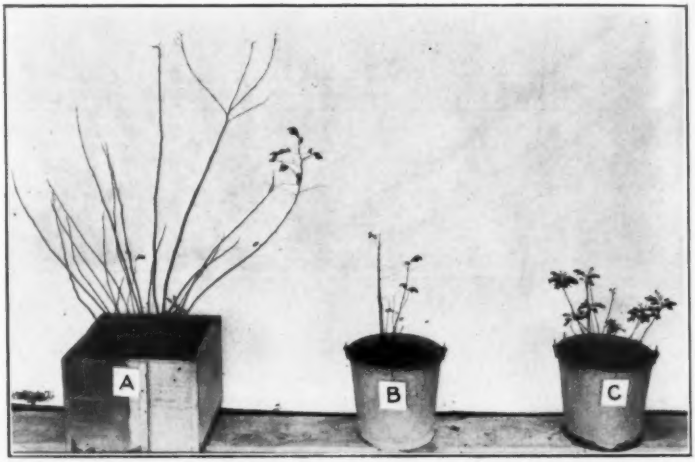

FIGURE 3.—Wild senna, *Cassia marilandica:* A, Control plants, which experienced the full length of day at Washington, D. C., and flowered each year, usually in July, from the beginning of the test in 1922 to 1930; B and C, plants given, respectively, 12 and 10 hours of daylight each day throughout the growing season beginning in 1922, and which never flowered; they barely maintained themselves each year

were observed: 1922, July 21; 1925, August 4; 1928, July 11; 1929, July 15; 1930, July 23.

DISCUSSION AND CONCLUSIONS

As a result of the preceding data, it is concluded that an unfavorable length of day does not merely temporarily inhibit flowering but may hold the plant in a nonflowering condition as long as short days are allowed to operate. On the other hand, a long period of suppressed flowering has shown no tendency to develop a persistent condition of nonflowering, nor has it left any impress toward delayed flowering when the plants have been again exposed to long days favorable to the flowering impulse. It is shown that flowering can be completely suppressed for many years, and there is no reason to suppose that a continuation of the experiments would fail to suppress flowering after many more years had elapsed or until the plants lost their vigor and died.

While the sedums have appeared to maintain themselves in a vigorously growing vegetative condition from year to year, although unable to flower under short-day conditions, the wild senna plants have given indications of a less successful adaptation to the long-continued short-day conditions. These latter plants have suffered severely, owing to the very poor development of vegetative stems, together with an enforced early senility and death, which normally closes a long period of active vegetative vigor and flowering where long days have been experienced. In this particular plant (wild senna) the attainment of flowering and seed production is accompanied by rapid and vigorous stem growth where long days are experienced, resulting in an efficient photosynthesis and an active translocation of reserve material to the underground storage parts to support the next year's growth. Continuous short-day treatments not only prevent flowering but lead to conditions of dormancy and senility before sufficient reserves have been accumulated for growth in subsequent seasons.

These experiments have a practical bearing on interpretations of the behavior of new plant introductions. It is evident that failure to flower, which in the past was usually attributed to unfavorable soil or temperature conditions, may be due to lengths of day unfavorable to flowering.

It is indicated that a wild plant in its natural invasions from an original center of occurrence must find itself subjected to the factor of length of day during the growing season as well as to other climatic and soil conditions. If its distribution depends upon successful seed production, its limits of distribution must depend largely upon those conditions of summer day length favorable to successful flowering and the production of fertile seed. Whether it can maintain itself in a region unfavorable to flowering would depend upon whether natural methods of vegetative propagation are at its disposal and whether sufficient nutrition reserves can be maintained to support healthy growth in the plants from year to year.

MONODONTOMERUS AEREUS WALKER, BOTH A PRIMARY AND A SECONDARY PARASITE OF THE BROWN-TAIL MOTH AND THE GIPSY MOTH[1]

By C. F. W. MUESEBECK[2]

Senior Entomologist, Division of Forest Insects, Bureau of Entomology, United States Department of Agriculture

INTRODUCTION

Monodontomerus aereus Walker, a hymenopterous parasite belonging to the chalcidoid family Callimomidae, was first introduced into the United States in 1906 with importations of webs containing hibernating larvae of the brown-tail moth, *Nygmia phaeorrhoea* Donovan. These importations were being secured in connection with attempts to introduce into the New England area that had become infested by the brown-tail moth some of the parasites that contribute toward its control in Europe. The specialists of the Bureau of Entomology engaged in the work during that early period were somewhat uncertain regarding the status of *M. aereus*. The species was reared under conditions which indicated that it was a primary parasite of some importance in the pupae of the brown-tail moth and also in those of the gipsy moth, *Porthetria dispar* (L.); on the other hand, it was definitely proven to be secondary in certain cases. Information accumulated since that time appears to have shown that although it occasionally acts as an internal primary parasite, *M. aereus* normally develops as a hyperparasite and as such is nearly always ectoparasitic.

It is the purpose of this paper to discuss the life history and general behavior of *Monodontomerus aereus* and to present such data as are available concerning the host relations of the species. The files of the gipsy moth laboratory at Melrose Highlands, Mass., contain incidental notes on this parasite made over a period of more than 20 years by a number of different observers. Some of these notes have been of considerable assistance in the preparation of this paper, particularly those recording certain observations made by D. W. Jones from 1915 to 1917 and by A. B. Proper in 1929 and 1930.

REVIEW OF LITERATURE

First described by Walker (*13, p. 158*)[3] in 1834, *Monodontomerus aereus* received little attention until the importation of gipsy moth and brown-tail moth parasites into the United States was undertaken by the Bureau of Entomology. Ratzeburg (*10, Bd. 1, p. 177; Bd. 3, p. 222*), however, had in the meantime again described the species under the name *Torymus anephelus* and had recorded it as having been obtained from webs of the hibernating larvae of the brown-tail moth and also from pupae of (*Lasiocampa*) *Dendrolimus pini* L. The

[1] Received for publication Mar. 25, 1931; issued September, 1931.

[2] The writer is indebted to C. W. Collins, in charge of gipsy moth research for helpful advice in the course of this study and for criticism of the manuscript.

[3] Reference is made by number (italic) to Literature Cited, p. 459.

story of its introduction into New England from Europe and the early experiences with the species at the gipsy moth laboratory have been given in some detail by Fiske (*2, p. 43–45*) and by Howard and Fiske (*5, p. 245–250*). In addition, there have been occasional incidental references to *M. aereus* in publications of the Bureau of Entomology and of the experiment stations of some of the New England States, but for the most part these have merely recorded the distribution of the species or have referred to its behavior as a hyperparasite. Very brief biological notes have been given by Muesebeck and Dohanian (*8, p. 19–20*).

DISTRIBUTION

According to the records at the gipsy moth laboratory concerning the shipments from which it was obtained, *Monodontomerus aereus* is evidently widely distributed in Europe. It has been received in importations from various parts of Germany, Austria, Czechoslovakia, Hungary, Russia, Italy, France, the Netherlands, and Spain. In addition, it is recorded as having been obtained from gipsy moth pupae received from Japan in 1908.

After its first importation from Europe in webs of hibernating larvae of the brown-tail moth during the winter of 1905–6, and its liberation in eastern Massachusetts the following spring, *Monodontomerus aereus* dispersed at a very rapid rate. At the present time it occurs over the entire area infested by the brown-tail moth in the New England States, and it may have spread beyond these limits. As yet no attempts have been made to secure records of possible distribution outside the area over which the brown-tail moth occurs, and because of the habits of the parasite it is rather unlikely that such records would be obtained unless definite attempts at recovery were made. The attraction which the brown-tail moth and, to a lesser degree, the gipsy moth seem to exert upon *M. aereus* may tend to hinder its rapid distribution outside of the areas over which these species occur. However, its ability to develop independently of these at least suggests that it may ultimately become widely distributed in the United States.

DESCRIPTION OF THE ADULT

The females of *Monodontomerus aereus* (fig. 1)[4] range in length from 1.5 to 3.5 mm. Head transverse; temples and cheeks strongly receding; antennae inserted a little below middle of face, 13-segmented, with one ring joint, a 7-segmented funicle, and a 3-segmented club. Thorax moderately stout; pronotum large, although transverse; notauli complete; pronotum, mesoscutum, and scutellum punctato-reticulate or confluently punctate; apical fourth of scutellum set off by a distinct transverse furrow and finely longitudinally aciculate; propodeum short, with a median carina and broad, lateral longitudinal impressions; on either side of this median carina at base a small, more or less circular, smooth pit; anterior wing with marginal vein three times as long as postmarginal; stigmal vein short, somewhat curved; posterior coxae large, compressed; posterior femora rather stout, with a conspicuous tooth on the lower margin near apex. Abdomen ovate, stout; ovipositor sheaths two-thirds the length of abdomen. Head, thorax, and abdomen greenish black; wings hyaline, without a dusky spot in the stigmal region; all coxae and femora black; tibiae brown; tarsi paler.

The male is essentially like the female but averages a little smaller in size.

Monodontomerus dentipes Boh., a common parasite in the cocoons of certain sawflies, is superficially very similar, but differs in having a

[4] The figure of the adult was drawn by H. B. Bradford, of the Bureau of Entomology.

conspicuous cloud in the stigmal region of the anterior wing, and in the apical part of the scutellum being completely smooth and polished; there are other differences, but those mentioned will suffice to distinguish the two species.

LIFE HISTORY AND HABITS

HIBERNATION

Monodontomerus aereus hibernates as an adult; and, as is normally the case with species having this habit, only females survive the winter. The compact webs of the hibernating larvae of the brown-tail moth have generally been regarded as the preferred hibernation quarters for this parasite, but recent observations suggest that old cocoons of the same moth may be used to an even greater extent, at

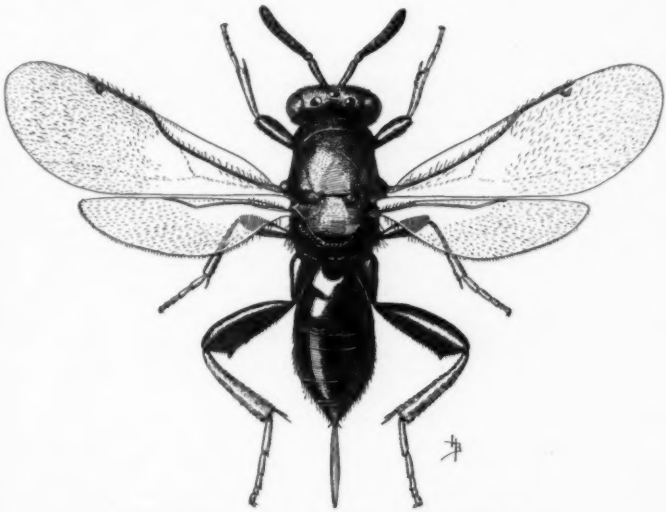

FIGURE 1.—Adult female of *Monodontomerus aereus*. × 17

least in areas where heavy infestations of that pest occur and where the cocoons are grouped together in compact masses on the trees or in the grass. Enormous numbers of hibernating females of *M. aereus* have been found in a relatively small quantity of such clusters of cocoons. Within these masses the empty pupal shells of *Nygmia phaeorrhoea* from which moths have issued seem to be particularly attractive, as many as 8 or 10 females of Monodontomerus being sometimes found packed together in one of them.

Howard and Fiske (*5, p. 250*) have remarked that this parasite exhibits "a distinct partiality for anything that savors of the brown-tail moth," and in so far as its search for winter quarters is concerned this seems to be true. A single specimen has been found hibernating in a bird's nest, and several have been obtained from old webs of the common fall webworm, *Hyphantria cunea* Drury. Furthermore, Muesebeck and Dohanian succeeded in carrying *Monodontomerus*

aereus through the winter in the folds of dried crumpled leaves (*8, p. 20*) as well as in old webs of the geometrid *Calocalpe undulata* (L.); and more recently the species has been successfully hibernated between layers of rather loosely rolled felting and in loose absorbent cotton. But it has been very difficult to find hibernating adults in the field except in the winter webs or old cocoon masses of the brown-tail moth. No doubt hibernation does occur in various situations, but apparently in no other quarters so commonly as in these.

According to the rather meager records available, winter mortality in some localities and under certain conditions may exceed 50 per cent, but owing to the complexity of the conditions bearing upon this and the small amount of information at hand, it is impossible to give figures that would even approximately represent the usual extent of such mortality.

In New England the females of *Mondontomerus aereus* usually issue from hibernation between the middle of April and the middle of May, the time of most general emergence being dependent principally upon temperature, although there is also considerable individual variation. In the same season and in the same locality some females have emerged as early as the 1st of May, whereas others have been found still in hibernation three weeks later. In the case of material held in a screened insectary at Melrose Highlands adults have issued from April 13 to May 17. They become active at temperatures of 65° F., or higher, and on any day, even very early, in the spring when the temperature reaches that point some females emerge from hibernation. But with a drop in the temperature they return temporarily to quarters that furnish some protection. Accordingly, at this time of year when occasional warm days are usually followed by several days of relatively low temperatures the parasites are only periodically active, and until after the middle of May they spend most of the time in seclusion.

OVIPOSITION

After the females of *Monodontomerus aereus* issue from hibernation, two or three weeks and often more elapse before they are ready to oviposit. A few eggs apparently ready for deposition have been found in the reproductive systems of some females as early as May 8, but numerous field observations and collections indicate that general oviposition does not begin normally until after the 1st of June. The earliest recorded observation of oviposition in the field concerns a female found attacking a cocoon of *Meteorus versicolor* (Wesm.) on May 27. That actual oviposition occurred in this case was demonstrated by the subsequent rearing of an adult of *M. aereus* from this cocoon.

The time required for the insertion of the ovipositor and oviposition varies considerably with the type of host and, in the case of some hosts, with the exact spot at which the ovipositor is inserted. Only 2 or 3 minutes are required for the female to pierce the delicate cocoons of *Apanteles lacteicolor* Vier., usually from 5 to 10 minutes are required to insert the ovipositor in tougher hymenopterous cocoons, such as those of *A. melanoscelus* (Ratz.) and certain Campopleginae, but often three-quarters of an hour will be taken to drill through the wall of a tachinid puparium or lepidopterous pupa unless the spot selected is in the softer integument between the segments, when only 15 or

20 minutes, or even less, may be required. The piercing of the wall of the host cocoon, puparium, or pupa is followed by more or less prodding about inside, varied by numerous complete insertions and partial withdrawals of the ovipositor. From 15 to 30 minutes may be consumed in these activities before the ovipositor is finally withdrawn and sheathed. In order to determine, then, if actual oviposition has occurred it is necessary either to hold the host material for emergence of *Monodontomerus aereus* or to open the cocoon, puparium, or pupa, as the case may be, and examine the contents, as the females frequently insert the ovipositor only for the purpose of providing an opening at which they may feed. Usually from one to four eggs are deposited before the ovipositor is withdrawn. If the host is a mature larva of a hymenopterous parasite contained in its cocoon or in the primary host pupa, or a tachinid that has reached the intrapuparial larval stage, as defined by Snodgrass (*12, p. 22*), the eggs of *M. aereus* are invariably placed externally upon the host. In the case of oviposition in parasite-free lepidopterous pupae, however, or in freshly formed tachinid puparia, in which the hardened cuticle of the puparium still adheres to the larval hypoderm, the eggs are deposited anywhere in the semifluid contents.

POTENTIAL REPRODUCTIVE CAPACITY

Little information has been obtained regarding the number of eggs that may be deposited by *Monodontomerus aereus*. However, in 1930 such a record was secured for each of five females that had hibernated at the laboratory. *Apanteles melanoscelus* and *Compsilura concinnata* Meig. were used as hosts, but owing to the relatively small numbers available not more than two cocoons or puparia could be introduced daily into each of the tubes containing the five isolated females. The hosts were usually left with the parasites for 24 hours and were then removed and dissected in order to determine the number of eggs that had been deposited. As shown in Table 1, the total number of eggs obtained from each of the five females ranged from 172 to 352, and oviposition extended over periods ranging from 43 to 56 days. With a more abundant supply of host material constantly accessible, the number of eggs deposited might have been greater and the period of oviposition possibly shortened. The largest number of eggs obtained on any one day from any of the females used in this experiment was 19; but it may be worth noting that a specimen employed in another experiment deposited 26 and 25 eggs, respectively, on successive days, these being the largest numbers recorded.

TABLE 1.—*Numbers of eggs deposited by each of five females of Monodontomerus aereus, Melrose Highlands, Mass., 1930*

Female No.	June																								July				
	2	5	6	7	8	9	10	11	12	14	16	17	18	19	20	22	23	24	25	26	27	28	29	30	1	2	3	4	5
1	2	0	0	0	0	2	3	12	7	6	0	0	0	11	13	16	8	13	18	0	12	10	7	7	3	0	0	0	3
2	0	3	8	5	5	6	9	7	7	12	11	9	0	8	9	14	0	0	0	0	4	12	0	0	0	10	7	5	4
3	0	2	5	2	5	7	6	4	4	9	2	4	3	9	4	6	0	9	8	4	6	12	11	7	7	2	2	5	3
4	1	4	4	5	9	6	5	7	6	8	5	0	4	9	0	11	7	4	0	0	0	8	0	0	6	5	7	4	3
5	4	4	5	6	5	10	8	6	5	13	7	9	0	4	7	9	0	8	0	0	0	0	0	0	0	0	7	5	6

TABLE 1.—*Number of eggs deposited by each of five females of Monodontomerus aereus, Melrose Highlands, Mass., 1930*—Continued

Female No.	July																									August				Total
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	5	
1	2	4	15	4	7	4	3	7	7	4	5	5	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	227
2	6	5	11	11	9	5	7	19	7	6	8	9	6	12	15	9	10	9	5	5	5	6	4	4	4	(a)	--	--	--	352
3	2	2	9	3	7	3	4	4	7	3	3	6	5	8	10	3	7	7	4	4	4	3	4	0	0	0	0	0	0	260
4	4	3	4	0	1	2	2	4	5	3	4	4	4	4	(a)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	172
5	4	7	11	14	5	2	2	3	5	(a)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	181

[a] Dead.

THE EGG

The egg of *Monodontomerus aereus* (fig. 2) measures from about 0.6 to 0.65 mm. in length and has an extreme width of about 0.2 mm. It tapers somewhat toward both ends and at one extremity is feebly produced. It is grayish white, the grayish tint being apparently due to the fact that the surface is thickly covered with very minute spines, one of which is shown much enlarged. The period spent in the egg stage normally covers from 48 to 72 hours, although at a temperature of 80° F., or higher, it may be even shorter than 48 hours.

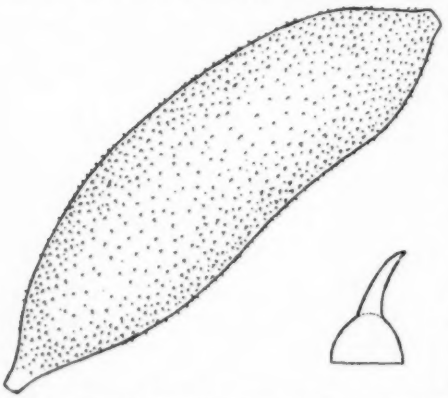

FIGURE 2.—Egg of *Monodontomerus aereus* × 145, and one of the spines very greatly magnified. These spines cover the surface of the egg

THE LARVA

The larva of *Monodontomerus aereus* passes through its five instars in rapid succession, the entire feeding period attemperatures of 75° to 78° F. covering only about four or four and a half days. In order to make possible the observation of the larval development in detail in certain individual cases several larvae were caused to develop in the cells of thick hanging-drop microscope slides, the concavities of which were 1.75 mm. deep. The hosts used in these cases were mature dormant larvae of *Apanteles melanoscelus* which had been removed from their cocoons. A single larva was placed in one of the slide cells, and an egg of *M. aereus*, dissected from a cocoon or puparium in which this parasite had been allowed to oviposit, was then transferred by means of a camel's-hair brush to the Apanteles larva, after which the cell was covered with a piece of thin celluloid that was held in place by means of a little shellac. With the Monodontomerus thus exposed to view it was possible to follow its development with the aid of a binocular microscope. After each molt the celluloid cover was removed from the cell and the cast skin transferred to a slide for mounting.

It has been found that the female normally kills or paralyzes host larvae before depositing eggs on them, but evidently this is not prerequisite to the successful development of the Monodontomerus larvae, for in the case of those parasites carried through in the slide cells the host larvae were living at the time the newly hatched parasite began to feed. In the few cases under observation it was noted that from 24 to 30 hours were spent in the first instar, from 10 to 18 hours in each of the second, third, and fourth instars, and from 100 to 120 hours in the fifth, although feeding ceased after only 24 to 36 hours had been passed as a fifth-instar larva. The meconium was cast about 60 hours after the cessation of feeding, and the last larval skin was molted off from 18 to 24 hours after the casting of the meconium.

The first instar larva is slender and tapers somewhat toward the posterior end. The head appears to be slightly more strongly chitinized than in the three succeeding instars though rather less so than in the fifth instar, and the well-chitinized mandibles are slightly bent. There are the usual 13 body segments, the last segment being short and more or less disklike, serving as an attachment sucker and enabling the larva to retain a firm hold upon the host. In this first instar there are four pairs of open spiracles, a pair each on the second thoracic and on the *first, second, and third abdominal* segments. On each body segment except the last there is a transverse row of long hairs, and mingled with these are two or three irregular rows of more closely placed but much shorter hairs. The last segment bears only the shorter hairs. When disturbed the larva raises itself erect upon its anal segment and then moves quite rapidly away, traveling with equal rapidity, in a succession of looping movements, either forward or backward.

The larvae of the succeeding instars do not differ strikingly from that of the first, except in size. However, the mandibles are not bent as in the first instar and are otherwise differently shaped. (Fig. 3.) Furthermore, there are nine pairs of open spiracles instead of four, these occurring on the second and third thoracic and the first seven abdominal segments; and the hairs on the body are relatively longer and more abundant, particularly in the case of the fifth-instar larva. The mature larva measures from 2.5 to 4 mm. in length.

THE PUPA

Since the mature larvae of *Monodontomerus aereus* do not spin cocoons, the pupae occur free in the puparium, cocoon, or pupal skin of the host, usually with the skin of the last larval molt attached to the posterior end. At first the pupa is white; it gradually darkens, however, and becomes black before the adult emerges. The time spent in the pupal stage normally covers 9 or 10 days.

EMERGENCE OF THE ADULT

The period from the time of deposition of the egg to the issuance of the adult from the host has been observed to range from 18 to 30 days, the average for more than 200 parasitized hosts, for which exact figures were obtained, being about 22 days. Usually the time covered by actual development is a little shorter than the periods just indicated, for the young adults of *Monodontomerus aereus* normally remain in the host 24 hours, and sometimes longer, before emerging. When ready to issue they cut roughly circular holes in the host envelope,

which are just large enough to permit the insects to pass through. Every adult, however, does not cut its individual hole, but several, and sometimes all, of the parasites in one host will emerge through the same exit hole. The number developing at the expense of a single host varies naturally with the size of the latter, but there is also a wide range in the number developing on host individuals of the same species and of similar size, from 1 to 24 adults, for example, having been obtained from a single puparium of *Compsilura concinnata*.

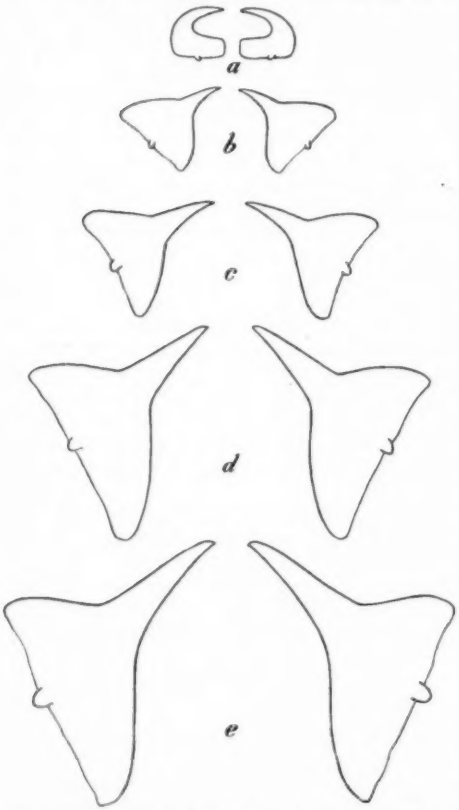

FIGURE 3.—Mandibles of larva of *Monodontomerus aereus*: *a*, of first-instar larva; *b*, of second-instar larva; *c*, of third-instar larva; *d*, of fourth-instar larva; *e*, of fifth-instar larva. All drawn to the same scale.

PROPORTION OF SEXES

Records are available concerning the numbers of each sex emerging from about 500 individual hosts representing several different species. Altogether 3,609 adults were obtained, and of these 2,220, or 61.5 per cent, were females, whereas only 1,389, or 38.5 per cent, were males. In the case of practically all lots of host material, either field-collected or parasitized in the laboratory, the number of females has been in excess of the number of males obtained.

MATING

Like other species of Chalcidoidea *Monodontomerus aereus* can reproduce without fertilization, but the progeny of such parthenogenetic reproduction are invariably males. Certainly under field conditions few, if any, females remain unfertilized. All of the numerous hibernating females that have been collected in the field and isolated for use in laboratory studies had been mated before entering hibernation, as evidenced by the occurrence of both sexes among the progeny of each one.

Adults of *Monodontomerus aereus* mate readily in confinement. The males are very eager to mate and will mate repeatedly with different females, although no instance has been observed of actual copulation with a female that had been previously mated. The males,

however, mount such females as well as those that are unmated and go through the rather extended preliminaries, consisting principally of prolonged tapping with the antennae, before attempting copulation. Actual coition requires at most but a few seconds. Mating will occur immediately after emergence, and it often takes place even before this, while the young adults are still inside the host envelope. Males have sometimes been observed to reenter the host puparia or pupae from which they had emerged to mate with females that had not yet issued.

FEEDING HABITS OF THE ADULTS

In the laboratory females of *Monodontomerus aereus* have been kept alive and in good condition for more than three months during the active period by holding them in clean containers and feeding them with a solution of one part of honey to four parts of water. And even some males have been held nearly as long. However, like many hymenopterous parasites, the female of *M. aereus* derives a considerable part of its nourishment from the hosts which it attacks. As already noted in the discussion of oviposition, the insertion of the ovipositor is not always followed by the deposition of eggs, and may only serve the purpose of providing a means of obtaining access to the fluid contents of the host. This habit of feeding at puncture holes made by the ovipositor has been so frequently observed and recorded in the case of many species of hymenopterous parasites, particularly since the publication of Howard's paper (*4*) on this subject, that an extended discussion of the habit in the case of *M. aereus* seems unnecessary.

The formation of feeding tubes by the females of certain species that have this habit of feeding at the puncture holes made by the ovipositor has also been capably discussed by several authors, including Lichtenstein (*6*), Genieys (*3, p. 179–180*), Parker and Thompson (*9, p. 455–457*), and Smith (*11, p. 588*). It may be worth noting, however, that the feeding tubes formed by *Monodontomerus aereus*, which extend from inside the body wall of the host itself to the outer surface of the cocoon, puparium, or pupa that has been punctured, appear to be less delicate than those observed in the study of some other species and are often very firmly attached to the host. They have frequently been found still in position on host larvae that had been removed from their cocoons or puparia after having been attacked and fed upon by *M. aereus*. The length of the tubes varies considerably, but the longest observed were about 0.8 mm. in length; in extreme diameter they were found to measure about 0.028 mm.

NUMBER OF GENERATIONS

In their brief notes on *Monodontomerus aereus*, Muesebeck and Dohanian (*8, p. 19*) stated: "There appear to be normally two generations annually, but the writers have carried the species through the full year with only one generation." Observations made since the publication of that statement, however, indicate that while two generations can often be obtained in the laboratory, and a small partial second generation appears to occur in the field, the species usually passes through only a single generation annually, 11 months, or more, being spent by the females in the adult stage, and most of this period in hibernation. They enter quarters that are used for hibernation very early, sometimes being found apparently in a dormant condition before the middle of August, but they emerge for

short periods intermittently throughout the autumn, sometimes even in November on warm days.

When there is a second generation oviposition may occur very soon after emergence and mating. No long period is required for eggs to develop, as is the case in the early spring after issuance from hibernation. Oviposition has been obtained as early as two days after emergence from the host.

HOST RELATIONS

Monodontomerus aereus has been reared from numerous different host species, but in some instances it has been impossible to determine with certainty whether it was actually parasitic upon the species from which it was reared or upon another parasite contained in that host. At the gipsy moth laboratory and at the European station of this laboratory, at Budapest, Hungary, *M. aereus* has been reared as a direct hyperparasite from a variety of hymenopterous and dipterous primary parasites of the gipsy moth and the brown-tail moth, including *Hyposoter disparis* (Vier.), *Meteorus versicolor, Apanteles melanoscelus, A. lacteicolor, A. liparidis* (Bouché), *Sturmia nidicola* (Towns.), *Compsilura concinnata, Tachina larvarum* L., and *Tricholyga segregata* (Rond.); and it has also been obtained from puparia of Sarcophagidae that were associated with dead gipsy moth larvae or pupae. In addition, it has been reared at Melrose Highlands from cocoons of *Iseropus coelebs* (Walsh), a common parasite of the white-marked tussock moth, *Hemerocampa leucostigma* S. and A. In all of these cases the hyperparasitic relationship of *M. aereus* is clear.

The species has, however, also been reared at Melrose Highlands from the pupae of certain Lepidoptera, most commonly from those of *Porthetria dispar* and *Nygmia phaeorrhoea*, and very rarely from pupae of *Hemerocampa leucostigma, Malacosoma americana* (Fab.), and *Cacoecia argyrospila* Walk. In addition it has been obtained in Europe from chrysalids of *Aporia crataegi* (L.) (*7, p. 70*), and from pupae of *Dendrolimus pini* (*10, Bd. 3, p. 222*) and *Evetria resinella* L.[5] In all such cases *Monodontomerus aereus* may have been either primary or secondary. To determine the exact relationship with certainty is often very difficult, for the remains of another parasite which may have served as the real host of Monodontomerus may be so reduced and so embedded in the cast larval and pupal skins and the excreta voided by the hyperparasitic larvae as to be practically unrecognizable, even in the course of a careful examination. The fact that in most cases remains of another parasite, which had been the true host, have eventually been found, has gradually led to the belief that *M. aereus* is always hyperparasitic, and that the failure always to find the remains of another parasite is due to the difficulty of recognizing them. Furthermore, to most students of the behavior of insect parasites it has seemed very unlikely that a single species could develop both as an ectoparasite, as *M. aereus* had been observed to do when parasitic in cocoons of other hymenopterous parasites and puparia of Tachinidae, and as an endoparasite, as it must necessarily do if a primary parasite in lepidopterous pupae. Cushman (*1, p. 42–43*), commenting on the recorded internal and external parasitism

[5] Specimens in the U. S. National Museum are labeled as having been reared from this host at Eberswalde, Germany, by Prof. K. Eckstein.

by a species of Theronia, probably expressed the rather general feeling on this point when he stated that it seemed "impossible that a parasite can be both internally and externally parasitic," and added that in his opinion "the remains of the true primary were simply not found" in those instances where Theronia was supposed to have been primary.

Recent studies at the gipsy moth laboratory have demonstrated, however, the essential correctness of the statement by Howard and Fiske (*5, p. 249*) that the larvae of *Monodontomerus aereus* "feed externally upon the pupae of tachinids within the puparium, but internally within the pupae of Lepidoptera." Numerous small lots of parasite-free pupae of the brown-tail moth and of the gipsy moth were placed in cages containing females of *M. aereus* that had been ovipositing, and were left for periods varying from three hours to several days. The oviposition cages used were tight wooden boxes, measuring about 9 by 5 by 4 inches, and provided with a sliding glass cover and in one end a stoppered opening 1½ inches in diameter through which the parasites and the host material, as well as food, could be introduced. Most frequently attempts of the females to insert their ovipositors were unsuccessful, for the parasites were easily and quickly dislodged by the movements of the pupae. In a relatively small number of cases oviposition occurred, but not all of the pupae in which eggs were actually deposited produced adults of *M. aereus*. Dissection of those pupae which had been attacked but from which no parasites emerged showed that frequently the Monodontomerus larvae had developed to maturity but had died without having pupated.

Of 127 parasite-free pupae of the brown-tail moth, which were introduced in lots of 3 to 10 at one time into cages containing from 50 to 75 *Monodontomerus aereus* females and left for periods varying from 5 to 50 hours, 116 ultimately produced moths. Six of the remaining eleven died of unknown causes, and five were parasitized by Monodontomerus. None of these five pupae produced adults of the parasite, however. One was dissected three days after introduction into the oviposition cage and found to contain newly hatched larvae of *M. aereus* which were feeding as internal parasites, and in each of the other four parasitized pupae the parasitic larvae developed to maturity but failed to pupate. Another lot of 27 pupae of the brown-tail moth, also known to be parasite free, was left with about 35 females of *M. aereus* for several days. Of these pupae 5 eventually produced from 6 to 37 Monodontomerus adults each.

Parasite-free gipsy moth pupae were also exposed to attack, lots of two to six being introduced at one time. In one experiment 111 pupae were submitted in this way. Fifty-eight of these produced moths, and 13 yielded adults of *M. aereus*; 4 others, on later dissection, were found to contain dead Monodontomerus larvae in varying degrees of development; while the remainder of the pupae were recorded as dead from unknown cause, no evidence of parasitism being noted. Several of those pupae which produced adults of the parasite were found, on being opened later, to contain varying numbers of dead mature larvae of *M. aereus*.

Inactive pupae of the gipsy moth containing nearly mature larvae of the tachinid parasite *Sturmia scutellata* (R. D.) were likewise submitted to Monodontomerus females. All were immediately attacked,

in some instances from 8 to 12 females being observed with ovipositors inserted in a single pupa. In all cases, however, the tachinid maggots later issued and formed puparia; and subsequent dissection of the puparia showed none of these to be parasitized.

Monodontomerus aereus has been reared only occasionally from field-collected pupae of the gipsy moth and the brown-tail moth in New England. Owing to the personal discomfort attending the handling of cocoons of the brown-tail moth, the pupae have usually not been removed from the tightly woven cocoons containing them in the case of collections made for the recovery of certain parasites. Accordingly Monodontomerus emerging from those collections can not be regarded as having always issued from these pupae, for often the cocoons contained puparia of Tachinidae at the time of collection, and these are known to be very freely attacked by *M. aereus* in the field. Annual collections of cocoons were secured from representative towns of the infested area for several years during the early period of the brown-tail-moth investigations conducted by the Bureau of Entomology. In 1913 a total of 3,746 cocoons were obtained in 52 separate collections, and from these 3,514 Monodontomerus were reared. After emergence had ceased the material remaining in the cages was examined. The cocoons were found to contain 525 puparia of *Compsilura concinnata*, of which only 72 had produced adults of the tachinid. Unfortunately the records are not complete and do not indicate the number of puparia that had exit holes of *M. aereus*, but it is very probable that the greater part of the Monodontomerus emerged from the Compsilura puparia. Throughout the entire series of collections the number of *M. aereus* secured varied directly with the number of puparia occurring in the cocoons of each collection. A detailed examination of the pupae in one collection showed that in some cases this parasite had also developed upon larvae of Ephialtes and Labrorychus that were present in the pupae of the primary host, but these species occurred so rarely that they could have accounted for only a small part of the *M. aereus* that emerged.

In 1930 a total of 2,164 pupae of the brown-tail moth were collected by members of the laboratory staff from 15 towns in Massachusetts New Hampshire, and Maine, removed from their cocoons, and isolated in small glass vials. Only 33 of these produced adults of *Monodontomerus aereus*, but 12 others were found, on later dissection, to contain dead mature larvae of the parasite. On an examination of the contents of the 33 pupae from which Monodontomerus had emerged, this parasite was observed to have been apparently primary in 16 cases, whereas in each of the remaining pupae the larvae of *M. aereus* had developed upon the larva of an ichneumonid, probably *Itoplectis conquisitor* (Say) or *Ephialtes pedalis* (Cress.), which already occupied the pupa at the time of oviposition by Monodontomerus.

From pupae of the gipsy moth collected in New England infestations *Monodontomerus aereus* has been obtained even less frequently than from those of the brown-tail moth. The files of the gipsy moth laboratory record the rearing of this parasite in small numbers from several collections of gipsy moth pupae in earlier years, sometimes from collections from which no other parasites were obtained, but during the past 10 years *M. aereus* has not been reared from that host, although many thousands of pupae have been collected and held for records of parasitism. On the other hand, similar collections obtained

in certain European infestations of the gipsy moth have occasionally produced Monodontomerus in some numbers. Examination of the contents of pupae producing the parasites showed, however, that in most cases *M. aereus* had developed in puparia of *Tachina larvarum* and *Tricholyga segregata*, two European tachinid parasites, not yet established in the United States, that very often form their puparia within the pupae of the host species.

In laboratory experiments cocoons of the hymenopterous parasites *Apanteles melanoscelus*, *A. lacteicolor*, *Spilocryptus nuncius* (Say), *Hyposoter disparis*, and *Meteorus versicolor* have been exposed to attack by *Monodontomerus aereus*, and reproduction has been obtained on all of these species. Numerous dissections have shown Monodontomerus to be ectoparasitic without exception when developing in cocoons of such parasites, and this has also been found to be the case when hymenopterous parasites that are contained within the pupae of the primary host are attacked.

Many puparia of *Compsilura concinnata*, and a few of those of *Sturmia nidicola* and *Carcelia laxifrons* Vill., have been submitted to *Monodontomerus aereus* in the laboratory, and they have always been attacked very readily. Dissections have demonstrated that the eggs are nearly always deposited externally upon the tachinid within the puparium and that Monodontomerus develops as an ectoparasite. When puparia that were only two or three hours old were submitted, however, the eggs were deposited in the semifluid contents, as already mentioned under "Oviposition," and later dissections showed the larvae to be developing as internal parasites. Quite frequently the Monodontomerus that had thus been forced to feed endoparasitically died after attaining larval maturity, being unable to pupate, just as in the case of some of those that developed as primary parasites in the pupae of the brown-tail moth and the gipsy moth. It is not altogether clear why death should so often occur in these cases after the larvae have become full grown, but it may be that sucessful pupation requires drier conditions than those which have been observed often to exist in pupae or puparia in which larvae of *M. aereus* developed as internal parasites.

ECONOMIC IMPORTANCE

The ability of *Monodontomerus aereus*, which is normally ectoparasitic, to develop as an internal parasite is of interest, but certainly the data available indicate that the internal primary parasitism by the species in lepidopterous pupae is of no practical significance.

Owing to the fact that the cocoons of hymenopterous parasites, and more especially the puparia of Tachinidae, are usually difficult to collect in the field, the numbers for which exact records of secondary parasitism have been obtained are very small in most cases. Three hymenopterous parasites, the cocoons of which have been collected by the gipsy moth laboratory over a period of several years, are *Apanteles lacteicolor* and *Meteorus versicolor*, both parasitic in the larvae of the brown-tail moth, and *A. melanoscelus*, a larval parasite of the gipsy moth. Parasitism by Monodontomerus has been practically negligible in the case of all three species. From 1,884 cocoons of *A. lacteicolor* only 14 *Monodontomerus aereus* were reared, while 7 out of a total of 1,040 cocoons of *M. versicolor* and 8 of a total exceeding 20,000 cocoons of *A. melanoscelus* produced this hyperpara-

site. There are many specimens of *M. aereus* in the laboratory collection which were reared from cocoons of *Hyposoter disparis* received from Italy in 1911 and 1912, but the records do not clearly show the proportion of cocoons parasitized. Ichneumonid parasites, such as species of Ephialtes, Itoplectis, and Theronia, contained within the pupae of the gipsy moth and the brown-tail moth, have also been found rather heavily parasitized by Monodontomerus, but since these primary parasites are only minor factors in the control of these hosts, the effect of the hyperparasitism is probably unimportant.

The numbers of tachinid puparia collected and isolated for records of hyperparasitism have been smaller, but parasitism by *Monodontomerus aereus* has been much heavier than in the case of the hymenopterous cocoons. Only 606 puparia of *Compsilura concinnata* and 1,088 puparia of *Sturmia nidicola* were collected in infestations of the brown-tail moth in New England over a period of four years. However, 225, or 37 per cent, of the puparia of *C. concinnata*, and 106, or about 10 per cent, of those of *S. nidicola*, produced *M. aereus*. Puparia of *Tachina larvarum* and *Tricholyga segregata* collected in European infestations of the gipsy moth were also heavily parasitized by Monodontomerus, but the records are incomplete and figures on the degree of parasitism can not be given. Furthermore, it has been observed in the laboratory that females of *M. aereus* kill many tachinids by direct feeding although no eggs may be deposited. The failure of a large proportion of field-collected puparia to produce adults of either the tachinid or the hyperparasite may be attributable in part to this habit.

In conclusion it may be stated that *Monodontomerus aereus* is probably not a hyperparasite of sufficient importance to cause much concern, but with conditions favoring its successful hibernation and reproduction it may locally become a serious enemy of certain species of Tachinidae which form their puparia in the cocoon masses of their hosts, or at least do not enter the soil to pupate. It may also considerably reduce the effectiveness of certain hymenopterous pupal parasites that pass through their transformations to pupa and adult within the host.

SUMMARY

Monodontomerus aereus Walker, a hymenopterous parasite of the chalcidoid family Callimomidae, was introduced into the United States from Europe in 1906 with hibernation webs of the larvae of the brown-tail moth. It is widely distributed in Europe, occurring from Russia to Spain and from the Netherlands to Italy. First liberated in Massachusetts in 1906, it now occurs throughout the area infested by the brown-tail moth in the New England States.

The adult female, which is a small, greenish-black, four-winged fly with toothed posterior femora and an ovipositor two-thirds as long as the abdomen, hibernates in old cocoon masses or winter webs of the brown-tail moth. Emergence from hibernation occurs in April and May, but general oviposition appears not to begin until after the 1st of June. From one to four eggs are deposited during one insertion of the ovipositor. These are usually placed externally on the host within the cocoon, puparium, or pupa, but when oviposition occurs in living lepidopterous pupae or very fresh tachinid puparia the eggs are deposited internally. From 172 to 352 eggs

have been obtained from isolated females ovipositing over periods ranging from 43 to 56 days.

The egg is elongate, grayish-white, and covered with minute spines. It normally hatches after from 48 to 72 hours; and the larva, which passes through five instars, usually becomes full-grown after 4 or 4½ days but does not pupate until several days later. The first-instar larva is slender, with a chitinized head and a 13-segmented body; the second, fourth, fifth, and sixth segments each have a pair of open spiracles, and all body segments are provided with transverse rows of conspicuous hairs. The later instars differ from the first principally in the size of the larva, in the size and shape of the mandibles, and in the larva's being more strongly hairy. The pupal stage, which is passed in the host envelope, covers 9 or 10 days, and the entire period from egg deposition to emergence of the adult an average of 22 days.

Records on the sex of 3,609 adults obtained from about 500 hosts showed 61.5 per cent to be females. Mating frequently occurs before the adults have emerged from the host. Like many other hymenopterous parasites, the females of *Monodontomerus aereus* commonly feed at the puncture holes made by the ovipositor, taking up the fluid contents of the host through a feeding tube.

Normally there is but one generation annually, about 11 months being passed in the adult stage, but there may be a small partial second generation. The females sometimes enter hibernation quarters early in August, although emerging intermittently until late autumn in order to feed.

Monodontomerus aereus has been reared as a direct hyperparasite from cocoons or puparia of many primary parasites of the gipsy moth and the brown-tail moth. It has also been obtained from the pupae of certain Lepidoptera, and in these cases has sometimes been a primary and sometimes a secondary parasite. In laboratory experiments it has been found to develop occasionally as an internal parasite in fresh tachinid puparia as well as in the pupae of the gipsy moth and the brown-tail moth, but normally *M. aereus* is an ectoparasitic hyperparasite and is sometimes a serious enemy of certain species of Tachinidae.

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THE CORRELATION BETWEEN STAND AND YIELD OF ALFALFA AND SWEETCLOVER[1]

By C. J. WILLARD

Associate in Agronomy, Ohio Agricultural Experiment Station

INTRODUCTION

There is a decided lack of exact data on the relation between stand and yield of forage crops which are sown broadcast. They are, to be sure, a considerable number of rate-of-planting tests with most forage crops, but these experiments usually do not report quantitatively the stand actually secured. A general relation between stand and yield is obvious to the most casual observer, but beyond that little is known.

A considerable amount of experimental work with forage crops has been done by the Ohio Agricultural Experiment Station at, and in cooperation with, the Ohio State University, in which yields of tops and roots have been determined by harvesting square-yard samples. In each instance the number of plants in the square yard has been counted. In many instances two or more square yards have been harvested from the same plot, or plots which had been treated alike. These replicated samples have actually differed in both yield and stand, and so furnished an opportunity to determine the extent to which the variations in yield of these small areas of forage crops were correlated with variations in stand.

EXPERIMENTAL RESULTS

Altogether, from 1923 to 1929, data were secured from 520 samples of alfalfa and 421 samples of sweetclover, two to five samples being taken from the same or comparable plots. These samples were distributed in 228 and 160 means, respectively. The yield of tops, the yield of roots, and the stand of each square yard included in each mean were expressed as percentages of that mean yield or stand. Correlations between yield of tops, yield of roots, and stand were then determined. The correlation figures are given in Tables 1 to 6. The divisions between the classes were made on the even 10 per cent; e. g., the class 100 to 109 contains all percentages from 100.00 to 109.99, inclusive. Sheppard's correction has been used in all computations. The constants secured are summarized in Table 7.

In calculating the standard deviations given in Table 7, n was reduced by the number of means around which the samples varied, or, specifically, $\sigma = \sqrt{\frac{\Sigma \text{ dev.}^2}{520-228}}$, and $\sigma = \sqrt{\frac{\Sigma \text{ dev.}^2}{421-160}}$, for alfalfa and sweetclover, respectively.

In addition to the standard deviations and correlation and regression coefficients, the standard deviations of the yields of tops and roots with stand held constant, or with the influence of variation due

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to stand removed, ${}_s\sigma_t$ and ${}_s\sigma_r$, respectively, were calculated from the formula ${}_s\sigma_t = \sigma_t \sqrt{1 - r^2_{st}}$. The term $\sqrt{1 - r^2_{st}} \times 100$ gives the percentages of the total variation that would remain if the observed yields were corrected for regression on stand by the coefficients secured in these experiments. These percentages are also reported in Table 7.

TABLE 1.—*Data for determining statistical correlation constants between yield of alfalfa tops and stand*

Stand (per cent of mean)	Number of samples of tops falling into percentage yield class indicated											Total
	Below 60	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	Above 150	
Above 150										1		1
140–149									1			1
130–139					4	1	2		1			8
120–129				2	4	9	7	2				24
110–119			2	13	22	33	18	5	4	1		98
100–109		5	9	12	33	43	20	8	1	1	1	133
90–99	2		7	21	40	31	13	8	5			127
80–89	1	4	4	16	31	23	9	2	1			91
70–79			1	8	10	4	3		1			27
60–69		1	1	2		4						8
Below 60		2										2
Total	3	12	24	74	144	148	72	25	14	3	1	520

TABLE 2.—*Data for determining statistical correlation constants between yield of alfalfa roots and stand*

Stand (per cent of mean)	Number of samples of roots falling into percentage yield class indicated											Total
	Below 60	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	Above 150	
Above 150									1			1
140–149									1			1
130–139						3	2	2	1			8
120–129					1	9	12	2				24
110–119				2	25	43	22	4	2			98
100–109	1		1	11	45	52	18	4	1			133
90–99		1	6	15	48	47	8	1		1		127
80–89		2	2	20	37	26	4					91
70–79		1	3	10	9	4						27
60–69		1	4	1	2							8
Below 60	1	1										2
Total	2	6	16	59	167	184	66	13	6	1		520

TABLE 3.—*Data for determining statistical correlation constants between yield of alfalfa tops and yield of roots*

Yield of alfalfa roots (per cent of mean)	Number of samples of tops falling into percentage yield class indicated											Total
	Below 60	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	Above 150	
Above 150												
140–149					1							1
130–139			1	1		1			2	1		6
120–129					4	2	4	3				13
110–119				5	11	19	19	8	3	1		66
100–109		1	5	21	52	68	23	6	6	1	1	184
90–99	2	4	8	24	57	45	19	7	1			167
80–89	1	4	5	18	15	9	6		1			59
70–79			5	5	2	3			1			16
60–69		2			2		1	1				6
Below 60		1				1						2
Total	3	12	24	74	144	148	72	25	14	3	1	520

TABLE 4.—*Data for determining statistical correlation constants between yield of sweetclover tops and stand*

Stand (per cent of mean)	Number of samples of tops falling into percentage yield class indicated											Total
	Below 60	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	Above 150	
Above 150			1		2	1	1	1				6
140–149					3		1	1	1	1		7
130–139				2	2	9	7	3	4		1	28
120–129	1			2	3	7	8	1	1			23
110–119			2	11	12	18	8	5	1			57
100–109			2	8	16	35	12	2	2		1	78
90–99	2	2	7	18	23	21	11	4	1	1		90
80–89		4	6	11	17	10	13	3				64
70–79	1	1	3	9	11	9	4	1	1	1		41
60–69		4	2	4	4	3	1	1				19
Below 60		1	1	1	2	2		1				8
Total	4	12	24	66	95	115	66	23	11	3	2	421

TABLE 5.—*Data for determining statistical correlation constants between yield of sweetclover roots and stand*

Stand (per cent of mean)	Number of samples of roots falling into percentage yield class indicated											Total
	Below 60	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	Above 150	
Above 150				2			2	2				6
140–149				1	1		2		2		1	7
130–139			1	1	1	9	7	4	5			28
120–129				2	2	4	6	8	1			23
110–119		1	4	7	11	15	14	3	2			57
100–109		2		7	21	28	16	1	2	1		78
90–99	1	1	5	16	28	26	7	2	4			90
80–89	4	3	4	8	23	11	8	3				64
70–79		3	6	12	7	10	2	1				41
60–69		2	2	9	4	1	1					19
Below 60		1	1	5	1							8
Total	5	13	23	70	99	104	65	24	16	1	1	421

TABLE 6.—*Data for determining statistical correlation constants between yield of sweetclover tops and yield of roots*

Yield of sweetclover roots (per cent of mean)	Number of samples of tops falling into percentage yield class indicated											Total
	Below 60	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	Above 150	
Above 150								1				1
140–149											1	1
130–139	1					3	2	2	6	1	1	16
120–129	1			1	4	4	6	6	2			24
110–119			3	1	8	23	19	9	1	1		65
100–109		1		6	28	39	26	3	1			104
90–99		2	3	26	29	28	11					99
80–89		1	10	18	24	15	1	1				70
70–79		3	5	10		2		1	1	1		23
60–69	1	3	3	3	2		1					13
Below 60	1	2		1		1						5
Total	4	12	24	66	95	115	66	23	11	3	2	421

TABLE 7.—*Statistical constants obtained from the data in Tables 1 to 6*

Subscripts: t=Tops, r=roots, s=stand.

Constant	Alfalfa	Sweetclover	Constant	Alfalfa	Sweetclover
				Per cent	*Per cent*
r_{st}	0.28±0.04	0.29±0.04	σ_t	20.1	20.8
r_{sr}	.55± .03	.45± .03	σ_r	16.1	21.0
r_{tr}	.36± .03	.59± .03	σ_s	19.4	26.1
			$reg._{t.s}$	0.29±0.04	0.23±0.04
			$reg._{r.s}$	.45± .03	.36± .03
			$_s\sigma_t$[a]	19.3	19.9
			$_s\sigma_r$[b]	13.4	18.7

[a] $_s\sigma_t$=95.9 per cent of σ_t for alfalfa tops, $_s\sigma_t$= 95.7 per cent of σ_t for sweetclover tops.
[b] $_s\sigma_r$=83.4 per cent of σ_r for alfalfa roots; $_s\sigma_r$=89 per cent of σ_r for sweetclover roots.

CONCLUSIONS.

For alfalfa and sweetclover, the correlation between the yields of tops and the stand, 0.28 and 0.29, respectively, is very low. Variations in stand accounted for less than 5 per cent of the total variation in yield of tops as measured by the standard deviation.

The correlations between the stand and the yield of roots are much higher than those for the yield of tops, in both alfalfa and sweetclover, being 0.55 and 0.45, respectively. In these samples, variations in stand accounted for approximately 11 per cent of the variation in the yield of sweetclover roots, and nearly 17 per cent of the variation in the yield of alfalfa roots.

The regression of yield on stand is 0.29 per cent and 0.23 per cent for yield of tops, and 0.45 per cent and 0.37 per cent for yield of roots, of alfalfa and sweetclover, respectively, for each 1 per cent change in stand. Despite this definite relation, other errors of random sampling would cause a variability 83 to 96 per cent as great as the uncorrected figures, when or if the original figures were corrected for stand. This reduction is probably not sufficient to justify the correction, especially since the only remedy for other errors of random sampling, replication, will also reduce variations due to stand.

The correlation between the yield of tops and the yield of roots is much lower in alfalfa than in sweetclover, but is surprisingly low in both, 0.36 and 0.59, respectively. Evidently, it is decidedly unsafe to predict the yield of roots from the yield of tops. Since these low correlations were obtained from samples intended to be uniform, they indicate that within very small areas there are important variations n the factors affecting the relative proportion of roots and tops.

The probable error of a single square-yard sample in these experinents has been ±13.6 per cent and ±14.0 per cent of the yield of he tops, and ±10.9 per cent and ±14.2 per cent of the yield of the oots, for alfalfa and sweetclover, respectively.

STUNTING OF WHEAT CAUSED BY TILLETIA LEVIS AND T. TRITICI[1]

By H. A. RODENHISER
Assistant Pathologist, Minnesota Agricultural Experiment Station

INTRODUCTION

Spore character has been generally accepted as a criterion for the separation of the two species of stinking smut, *Tilletia levis* Kühn and *T. tritici* (Bjerk.) Wint. Difference in the degree of stunting caused by the two species also has been suggested as a basis for separation. There seems, however, to be more or less confusion in the literature regarding the accuracy of this latter criterion.

Harwood [2] observed a difference in height of wheat plants infected with *Tilletia levis* and *T. tritici* in Michigan. The plants infected with *T. levis* were found to be little if any shorter than uninfected plants, while those infected with *T. tritici* were considerably stunted. Potter and Coons [3] confirmed Harwood's observations and suggested still other differences in the host reaction to the two species, namely, differences in the general shape of infected spikes, in the number of apical florets infected, in the general shape of the bunt balls, and in the consistency of the chlamydospore mass within the bunt balls. Other investigators, however, have been unable to confirm Harwood's observation. Selby [4] in Ohio found no difference in the relative degrees of stunting, and McAlpine [5] in Australia likewise could find no perceptible difference in the height of plants infected with *T. levis* and those infected with *T. tritici*. At University Farm, St. Paul, Minn., the writer has noted for several years that plants grown in experimental plots and infected either with *T. levis* originally collected near St. Paul or with *T. tritici* originally collected near Brandon, Manitoba, have been approximately 5 to 15 cm. shorter than uninfected plants. Furthermore, no consistent differences in relative degrees of stunting of plants infected with these strains of *T. levis* and *T. tritici* have been observed.

In view of these conflicting observations it is apparent that marked differences in degree of stunting of wheat plants infected with *Tilletia levis* and *T. tritici* are not the same in the different wheat-growing areas. This not only suggests the importance of considering the effects of environmental conditions and the reaction of different wheat varieties, but also the host reaction to different physiologic forms of *T. levis* and *T. tritici* as regards differences in degree of stunting of the wheat culms.

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[1] Received for publication Apr. 27, 1931; issued September, 1931. Paper No. 1004 of the Journal Series of the Minnesota Agricultural Experiment Station.

[2] HARWOOD, P. M. SMUT IN OATS AND WHEAT; JENSEN OR HOT WATER TREATMENT. Mich. Agr. Expt. Sta. Bul. 87, 10 p., illus. 1892.

[3] POTTER, A. A., and COONS, G. H. DIFFERENCES BETWEEN THE SPECIES OF TILLETIA ON WHEAT. Phytopathology 8: [106]-113, illus. 1918.

[4] SELBY, A. D. SOME DISEASES OF WHEAT AND OATS. Ohio Agr. Expt. Sta. Bul. 97, p. 31-61, illus. 1898.

[5] MCALPINE, D. THE SMUTS OF AUSTRALIA, THEIR STRUCTURE, LIFE HISTORY, TREATMENT, AND CLASSIFICATION. 288 p., illus. Melbourne. 1910.

A study was made to determine the host reaction to *Tilletia levis* and *T. tritici* and to physiologic forms of these species in regard to differences in relative degree of stunting in three wheat varieties grown at University Farm, St. Paul, Minn.

MATERIALS AND METHODS

Three varieties of wheat, including two spring wheats, Kota, C. I.[6] No. 5878, and Little Club, C. I. No. 4066; and a winter variety, Minhardi, C. I. No. 5149, were used in the tests. These varieties were inoculated with the collections of *Tilletia levis* and *T. tritici* indicated in Table 1. The tests with Kota wheat were made in the summer of 1928 and with Little Club in the summer of 1929. Minhardi was sown in the fall of 1928 and the data recorded in the summer of 1929. Previous to inoculation, the seed was treated by Jensen's modified hot-water method. When thoroughly dry, the seed was inoculated with powdered inoculum from each collection at the rate of 0.5 gm. of smut spores to 100 gm. of seed, and sown in triplicate, systematically distributed, in rod rows, at University Farm, St. Paul, Minn. Mature plants of a single variety infected with bunt of a single collection in each of the replicated rows were pulled and bulked. Infected culms were then cut off at the crown of the plant and a random sample of 200 individuals taken. A similar random sample of uninfected culms was taken from check rows for comparison. Measurements of the length of culms, from the crown to the base of the spike, were recorded to the nearest centimeter. Differences in the relative degree of stunting were considered significant only when they were three or more times the probable error.

EXPERIMENTAL RESULTS

The results of the experiments are given in Table 1. From these data it is evident that both *Tilletia levis* and *T. tritici* caused stunting of Kota, Minhardi, and Little Club wheats. On Kota, *T. levis* caused an average reduction in the length of culms of 9.37 ± 0.8980 cm. and *T. tritici* an average reduction of 10.64 ± 0.8504 cm. Both species of bunt caused a still greater reduction in the average length of culms of Minhardi. On this variety the average reduction caused by *T. levis* was 18.52 ± 0.6511 cm. and by *T. tritici* 18.46 ± 0.6511 cm. Two physiologic forms of *T. levis* and two of *T. tritici* caused similar reductions in the average length of culms of Little Club. A form of *T. levis* collected at St. Paul, Minn., and a form of *T. levis* collected in Egypt reduced the length of culms 11.14 ± 0.6529 cm. and 9.72 ± 0.6378 cm., respectively. Likewise, a form of *T. tritici* collected in Pullman, Wash., and one collected in Norway reduced the length of culms 12.10 ± 0.5731 cm. and 8.67 ± 0.6010 cm., respectively.

It is also clear from the data presented in Table 1 that there were no significant differences in the degree to which *Tilletia levis* and *T. tritici* stunted the culms of either Kota or Minhardi wheats. On Kota the difference in the average length of culm of plants infected with *T. levis* and *T. tritici* was 1.27 ± 0.8429 cm., while on Minhardi it was 0.06 ± 0.6788 cm. In both instances these differences are less than three times the probable error and are not considered significant.

[6] C. I. denotes accession number of Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

TABLE 1.—*Mean height of culms of Minhardi, Kota, and Little Club wheats inoculated with different collections of Tilletia levis and T. tritici, grown at University Farm, St. Paul, Minn.*

Variety	C. I. No.	Species of smut	Source of collection	Mean height
				Cm.
Minhardi	5149	*T. levis*	Minnesota (St. Paul)	67.13±0.48
		T. tritici	Manitoba (Brandon)	67.19± .48
		Uninoculated		85.65± .44
Kota	5878	*T. levis*	Minnesota (St. Paul)	63.90± .63
		T. tritici	Manitoba (Brandon)	62.63± .56
		Uninoculated		73.27± .64
Little Club *	4066	*T. levis*	Minnesota (St. Paul)	83.07± .50
		do	Egypt	84.49± .48
		T. tritici	Washington (Pullman)	82.11± .39
		do	Norway	85.54± .43
		Uninoculated		94.21± .42

* The physiologic forms of *T. levis* and *T. tritici* used on Little Club were originally identified in the following publication: RODENHISER, H. A., and STAKMAN, E. C. PHYSIOLOGIC SPECIALIZATION IN TILLETIA LEVIS AND TILLETIA TRITICI. Phytopathology 17:247–253, illus. 1927.

On Kota and Minhardi wheats the reaction to a single collection of *Tilletia levis* and of *T. tritici* were compared. On Little Club wheat the reaction to two physiologic forms of each species was studied. On this variety no significant difference was found between the average length of culms of plants infected with a form of *T. levis* collected at St. Paul, Minn., and a form of *T. tritici* from Pullman, Wash., the difference being only 0.96 ± 0.6341 cm. Likewise, the difference in the average length of culms of plants infected with a form of *T. levis* from Egypt and a form of *T. tritici* from Norway was only 1.05 ± 0.6444 cm. Significant differences were found, however, between the average length of culms of plants infected with the form of *T. levis* from St. Paul, Minn., and the form of *T. tritici* from Norway and likewise between those infected with *T. levis* from Egypt and *T. tritici* from Pullman, Wash. The differences in the average length of culms were 2.47 ± 0.6594 and 2.38 ± 0.6184 cm., respectively.

It is further evident from the data presented in Table 1 that there may be greater differences in relative degree of stunting between culms of plants infected with different physiologic forms of the same species than between those infected with *Tilletia levis* and *T. tritici*. The difference in the average length of culms of plants infected with the form of *T. tritici* from Pullman, Wash., and the form of *T. tritici* from Norway was 3.43 ± 0.5805 cm. This difference in relative degrees of stunting is greater than was found in any comparative test between species.

In addition to observing differences in relative degree of stunting caused by the two species of bunt, Potter and Coons[7] noted differences in the host reaction as regards the general shape of infected heads, the general shape of the bunt balls, and the consistency of the chlamydospore mass. In the present investigation, variations of this nature were observed, but they were not found to be consistent for a single species. In fact, these differences were just as marked between plants infected with different physiologic forms of the same species as between plants infected with *Tilletia levis* and *T. tritici*.

[7] POTTER, A. A., and COONS, G. H. Op. cit.

DISCUSSION AND CONCLUSION

It is clear from the data obtained that *Tilletia levis* as well as *T. tritici* may cause significant reduction in length of culms of wheat plants. Furthermore, whether or not there is a significant difference in the relative degree of stunting caused by the two species of bunt depends on the physiologic form of bunt with which the plant is infected. In one instance a greater difference was found in the relative degree of stunting caused by two physiologic forms of *T. tritici* than between *T. levis* and *T. tritici*. It is entirely possible that the physiologic forms tested might have reacted differently on other varieties and under different environmental conditions. However, in view of the data obtained, difference in relative degree of stunting of the host plant can not be generally accepted as a criterion for the separation of *T. levis* and *T. tritici* in the field. Furthemore, these data and the fact that different physiologic forms of bunt are known to occur in different geographical areas very probably explain the conflicting observations cited by several investigators in the United States and McAlpine in Australia relative to differences in degree of stunting caused by the two species of bunt.

SUMMARY

Both *Tilletia levis* and *T. tritici* may cause significant reduction in the length of culms of wheat plants.

Whether or not significant differences occur in the relative degree of stunting caused by *Tilletia levis* and *T. tritici* depends on the physiologic form of the species of bunt with which the plant is infected.

A greater difference was found in the relative degree of stunting caused by two physiologic forms of *Tilletia tritici* than between *T. levis* and *T. tritici*.

Differences in the host reactions as regards the general shape of infected heads, the shape of the bunt balls and consistency of the chlamydospore mass were observed but were not found to be consistent for a single species.

PENETRATION OF PETROLEUM OILS INTO PLANT TISSUE[1]

By JOSEPH M. GINSBURG[2]

Biochemist in Entomology Investigations, New Jersey Agricultural Experiment Station

INTRODUCTION

Foliage injury resulting from summer oil sprays offers a puzzling problem, the causes of which have not yet been definitely established. Although the saturated oils or the so-called "white oils" are less injurious by far than the unrefined light lubricating oils, they often bring about physiological disturbances[3] in the growth processes of plants after several successive sprays. The symptoms of injury from these oils are usually manifested by chlorotic areas in the leaves, dropping of foliage, dropping of fruit in the early part of the season, early blooming, retardation or hastening of the ripening processes of fruit, russeting of fruit, decrease in the size of fruit, and many other physiological changes.

Summer oil sprays possess specific merits in the control of orchard pests. They may serve directly as contact insecticides or indirectly as carriers for internal poisons which can be applied as arsenical substitutes, such as pyrethrum, nicotine, rotenone, etc. In view of the foregoing considerations the necessity for an oil that can be safely used on foliage is of great importance to the orchardist. An investigation was, therefore, undertaken to study the factors involved in oil injury and the possibility of their elimination.

Two theories suggested themselves which might explain the injury observed.

1. Absorption of sun light. It was conjectured that the oil coat on the surface of the leaf may absorb rays of certain wave lengths, beneficial to photosynthetic activity, preventing them from reaching the chloroplasts in the leaf. Spectrophotometric analyses, carried out during the last summer on apple and peach leaves covered with thin layers of white oils disclosed the fact that clear, refined oils such as those used for summer oil spraying absorb none of the visible rays ranging in wave lengths from 470 μ to 650 μ. Of the ultra-violet rays only those below 280 μ are absorbed. The ultra-violet rays of this wave length are not emanated from the solar spectrum and therefore play no part in the plant economy.

2. Penetration of oil. The injury characterized by dead areas in the leaf and drop of fruit and foliage suggests direct penetration of oil into

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[2] The author wishes to express his gratitude to Dr. T. J. Headlee for valuable advice given throughout the experiment.

[3] DE ONG, E. R., KNIGHT, H., and CHAMBERLIN, J. C. A PRELIMINARY STUDY OF PETROLEUM OIL AS AN INSECTICIDE FOR CITRUS TREES. Hilgardia 2: [351]–384, illus. 1927.

GINSBURG, J. M. OIL SPRAYS AND EMULSIFIERS. N. J. State Agr. Expt. Sta. Ann. Rpt. 47: 206–208. 1927.

——— WHAT SUMMER OIL SPRAYS MAY DO TO APPLE TREES. Jour. Econ. Ent. 24: 283–290, illus. 1931.

WOODWORTH, C. W. PETROLEUM INSECTICIDES. Jour. Econ. Ent. 23: 848–851. 1930.

living plant tissue. The work of Kelley [4] and others has shown that refined petroleum oils penetrate into leaves through stomata or otherwise. Kelley also found that penetration of oils into plant tissue affects respiration of foliage and dormant twigs.

This paper presents a study of the rate of penetration of various oils into plant tissue. Apple, peach, and tomato plants were used for this purpose.

EXPERIMENTAL WORK

Petroleum oils ranging in viscosity from 30 to 320 Saybolt/100 were selected for this purpose. In order to make the oils visible after they penetrated into the plant tissue they were stained red by incorporating 0.1 to 0.2 per cent Sudan III (an oil-soluble dye). The oils were tested in pure form and in emulsions containing about 3 per cent actual oil, powdered skim milk being used as emulsifier. This work was carried out during the winter and early spring months of 1929 and was repeated in 1930.

PENETRATION OF OIL INTO LEAVES

Tests on foliage were carried out in the following manner: Small droplets of oil, about 0.01 c. c., were deposited from a capillary pipette on the upper and under surfaces of leaves of several species of plants grown in the greenhouse, different leaves for each treatment being used. Observations were made on the time it took for the oil to penetrate through the epidermis and reach the interior of the leaf tissue. Where penetration took place the leaf tissue became translucent, and the red oil was distinctly visible on the surface opposite that upon which it was applied. When no penetration took place the oil remained on the surface where applied in the form of either a thin layer or a globule and was not pronounced on the other surface. When oil emulsions were tested the entire surface of the leaf was covered with the diluted emulsion by the aid of a camel's-hair brush.

In Tables 1 and 2 the rate of penetration is designated as slight, indicating irregular penetration through soft spots here and there in the epidermis; as partial, when penetration occurred in definite areas only, such as along the midribs or veins of the blade; and as complete, when the oil penetrated throughout the tissue making the entire area translucent.

In general, the observations suggest that oil penetrates readily through the epidermis covering the undersurface of the leaf and very slowly or not at all through the epidermis covering the upper surface of the leaf. When applied on the undersurface every one of the oils tested in pure form penetrated into the tissue, but the rate of penetration was indirectly proportional to the viscosity of the oil. When applied on the upper surface, only oils having a viscosity of 125 or lower reached the leaf tissue, the rate of penetration again being indirectly proportional to the viscosity, while oils having a viscosity of 160 or higher did not penetrate at all after 200 hours. Injury ranging from slight discoloration to brown or dead tissue occurred in every case where penetration took place.

[4] KELLEY, V. W. EFFECT OF CERTAIN HYDROCARBON OILS ON RESPIRATION OF FOLIAGE AND DORMANT TWIGS OF THE APPLE. Ill. Agr. Expt. Sta. Bul. 348, p. 371–406, illus. 1930.
——— EFFECT OF CERTAIN HYDROCARBON OILS ON THE TRANSPIRATION RATE OF SOME DECIDUOUS TREE FRUITS. Ill. Agr. Expt. Sta. Bul. 353, p. 581–600. 1930.

TABLE 1.—*Penetration of oil into Gravenstein apple leaves when applied on the upper surface of the leaf*

Oil No.	Viscosity (Saybolt/100)	Penetration of oil after—					Injury observed
		1 hour	24 hours	64 hours	120 hours	200 hours	
1	30	Complete					Dead tissue.
2	55	None	Slight through veins only.	Complete			Do.
3	81	do	Slight	Slight	Slight	Slight	Tissue transparent but not injured.
4	125	do	Slight along veins only.	do	do	do	Do.
5	145	do	None	None	do	do	Do.
6	160	do	do	do	None	None	None.
7	185	do	do	do	do	Slight	Do.
8	220	do	do	do	do	do	Do.
9	320	do	do	do	do	do	Do.

TABLE 2.—*Penetration of oil into Gravenstein apple leaves when applied on the undersurface of the leaf*

Oil No.	Viscosity (Saybolt/100)	Penetration of oil after—				Injury observed
		1 hour	48 hours	120 hours	200 hours	
1	30	Complete				Slight.
2	55	do				Dead tissue.
3	81	Partial	Complete			Distinct injury showing brown spots.
4	125	do	do			Do.
5	145	do	do			Do.
6	160	do	Partial	Partial	Complete	Slight injury, dead spots here and there.
7	185	do	do	do	do	Do.
8	220	do	do	do	do	Do.
9	320	do	do	do	do	Do.

These observations are significant and suggest that oils penetrate into the leaf tissue primarily through the stomata, since the latter are mostly located on the undersurface of the apple leaf. Results similar to those described above were also obtained with leaves of peach trees and tomato plants. The results clearly indicate that lubricating oils, even when highly refined (freed from unsaturated hydrocarbons) may cause injury to foliage by penetration. Efforts to reduce the rate of penetration through the undersurface either by increasing the viscosity or by incorporating inert materials into the oil have not thus far produced encouraging results. The chemicals tested for this purpose consisted of various gums, metallic soaps, rosins, colloidal clays, waxes, and ferric oxide.

The penetration of oil emulsions into foliage was somewhat similar to that observed for pure oil with the exception that a longer period of time was required. Even the lowest viscosity oil tested which completely penetrated both lower and upper surfaces of the leaf when applied in pure form, did not penetrate till after several hours. Oils of higher viscosities than 80 did not penetrate at all through the upper surfaces and very little through the undersurfaces, as revealed by microscopic examination. This can possibly be explained by the

fact that the actual amount of oil on the leaf is much greater when the oil is applied in a pure form than when applied as an emulsion. A more rapid rate of penetration should, therefore, be expected.

PENETRATION OF OILS INTO APPLE TWIGS

Studies of penetration of oil into apple twigs were made by the following two methods: (1) In order to determine whether oils are absorbed and conducted by the vascular bundles, the ends of young twigs from two varieties of apple trees (Gravenstein and Wealthy) were *immersed* in bottles containing various oils to a depth of 1 inch. After several hours, or when the leaves began to wilt, the twigs were removed, the surface of the bark was freed from oil, and cross sections were examined for the presence of oil; and (2) in order to determine whether oils penetrate through the young bark, another set of apple twigs was placed in bottles containing water to a depth of about 2 inches. Oil was then poured on the surface of the water to make a layer 1 inch thick. The water prevented wilting and allowed a longer period of time for observation. Twigs of uniform thickness, 8 inches long, were selected for these tests.

The results presented in Tables 3 and 4 indicate that apple twigs can absorb petroleum oils of viscosities ranging from 30 to 320 into the conductive tissue and carry them upward 7 inches or higher. Oils of lower viscosities, such as 30 and 55, can penetrate from the vascular bundles into the petioles of the leaves. In general, the rate of absorption of the various oils tested varied with viscosity. Twigs immersed in oils of viscosities ranging from 145 to 320 absorbed considerably less oil during 24 hours than did the twigs kept in oils of viscosities ranging from 30 to 125. The amounts of oil present could be compared approximately by the depth of red coloration of the tissue, brought about by the dye incorporated in the oil.

TABLE 3.—*Penetration of oil into 1-year-old apple twigs the ends of which were immersed 1 inch in oil*

Oil No.	Viscosity (Saybolt/100)	Penetration of oil after 24 hours
1	30	Vascular bundles saturated with oil throughout length of stem; oil also present in petiole and blades of leaves; no oil present in pith.
2	55	Oil present in conductive tissue throughout length of stem; present in petioles, but not in pith or blade.
3	81	Oil throughout vascular bundles; very slight amount in petioles.
4	125	Oil present in stem up to 6 inches high; the first 2 inches of conductive tissue contained considerably more oil than the upper 4 inches.
5	145	Do.
6	160	Do.
7	185	Oil present throughout conductive tissue in much lighter concentration than obtained with oils of lower viscosities.
8	220	Appreciable amount of oil in the first 2 inches but very light penetration in the higher areas.
9	320	Do.

TABLE 4.—*Penetration of oil into 1-year-old apple twigs the ends of which were immersed in water and 1 inch in oil*

Oil No.	Viscosity (Saybolt/100)	Penetration of oil after 24 hours
1	30	Oil present in phloem and cambium layer throughout the twig; none in the xylem.
2	55	Appreciable amount of oil present in phloem and cambium only in the area of stem in contact with oil; none in the xylem.
3	81	Slight amount of oil in cambium and phloem.
4	125	Traces of oil in phloem and cambium.
5	145	No oil in any part of the twig.
6	160	Do.
7	185	Do.
8	220	Do.
9	320	Do.

Oils ranging in viscosities from 145 to 320 did not penetrate at all through the young bark of the twig. Oils having viscosities of 81 and 125 exhibited only slight penetration through the bark. Only traces of these two oils were found in the phloem and cambium, corresponding only to the area of bark in contact with oil. An appreciable amount of oil having a viscosity of 55 was found both in the phloem and cambium corresponding only to the area in contact with the oil.

PENETRATION OF OIL EMULSION INTO APPLE TWIGS

The ends of 1-year-old apple twigs were immersed 1 inch deep in bottles containing oil emulsion diluted to 3 per cent oil. The bottles were frequently shaken or stirred in order to obtain uniform distribution of the oil. The height to which the oil had risen in the stem after 24 hours was then observed by splitting the bark and tracing the streams of red oil in the vascular bundles and other parts of the twig. The results, presented in Table 5, show that the oil emulsions were absorbed into and conducted by the vascular bundles to a much smaller extent than the oils in pure form. The only oil emulsions which rose to the height of 5 inches in the stem were the two of the lowest viscosities tested. Oils of 81 viscosity or greater were found only 2 inches high or less in the stem or approximately 1 inch above the oil emulsion level in the bottles. Evidently the conductive tissue in the apple twig possesses a selective absorption for water in preference to viscous oils when present in emulsified form.

TABLE 5.—*Penetration of oil into 1-year-old apple twigs the ends of which were immersed 1 inch in oil emulsions containing 3 per cent oil*

Oil No.	Viscosity (Saybolt/100)	Penetration of oil after 24 hours
1	30	Oil present in vascular bundles 5 inches high.
2	55	Oil present in vascular bundles 4 inches high.
3	81	Oil present in vascular bundles 2 inches high; the amount of oil less than in No. 2
4	125	Oil present in vascular bundles 2 inches high.
5	145	Do.
6	150	Oil present in vascular bundles 1.7 inches high.
7	185	Oil present in vascular bundles 1.5 inches high.
8	220	Do.
9	320	Oil present in vascular bundles 2 inches high.

In general, these results indicate that the vascular bundles of the apple stem can absorb and conduct petroleum oils to a considerable height. The rate of translocation like that of penetration, is indirectly proportional to viscosity and directly proportional to the concentration of the oil, since the twigs absorbed larger amounts of oil in pure form than from 3 per cent emulsion. Very little of the oil, however, reaches the conductive tissue through the cork of the stem when sprayed with emulsified petroleum oils possessing higher viscosities than 55 Saybolt and the danger of plant injury from this angle is rather small. Penetration of all petroleum oils, thus far tested, into foliage seems to be a general phenomenon. The penetration takes place primarily through the undersurface, presumably through the stomata, and only to a very limited extent through the upper surface of the leaf. Apparently penetration is one of the contributing causes for tree injury resulting from summer oil sprays, since wherever penetration occurred the leaf tissue was more or less injured.

SUMMARY AND CONCLUSIONS

Refined petroleum oils of various viscosities, stained red with an oil-soluble dye, were applied on the upper and lower surfaces of leaves of apple, peach, and tomato plants. The time it took for the oil to penetrate into the leaf tissue was observed. The same oils were also tested on apple twigs. The following conclusions can be drawn from the results obtained:

All the various oils tested penetrated through the undersurface of the leaf, presumably through the stomata, the rate of penetration varying indirectly with the viscosity of the oil.

Only oils of low viscosity penetrated through the upper surfaces of the leaf. Oils of higher viscosities did not penetrate at all, or only slightly, through the upper surfaces of leaves.

Wherever oil penetrated into the leaf injury followed shortly after.

Penetration of emulsified oils is much slower and is accompanied with less injury than that of pure oils.

Petroleum oils are absorbed and conducted by the vascular bundles of apple twigs, the rate of conduction varying indirectly with the viscosity of the oil.

The viscous oils either do not penetrate at all, or only to a very slight extent, through the outer cork of the twig. Only oils of very low viscosities exhibited appreciable penetration through the cork and into the cambium of the apple twig.

Penetration of oil into leaf tissue as well as absorption into apple twigs vary directly with the concentration of the oil.

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